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The potential impact of seal and seabird predation on North American Atlantic salmon

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ABSTRACT

This paper seeks to determine whether seal and seabird predation could have caused the major decline in pre-fishery abundance of North American Atlantic salmon. Growth rates of marine-phase salmon were modeled as a series of logistic curves. Numbers of salmon alive were modeled by applying a size-based mortality function to estimates of North American smolt runs and subsequent adult pre-fishery abundance. The biomass of North American post-smolts estimated for the 1990s increased sharply during the summer to peak at 1,400-1,800 t in late fall.

Windows of predation vulnerability were taken as periods when salmon and seals or seabirds spatially co-exist, and salmon are of a size taken by the predator. All seals and seabirds considered in this paper take smolt-size prey. Seals take marine-phase salmon of all sizes, but birds are constrained to smaller prey, and post-smolts outgrow predator capability by mid-June to fall, depending on the species. Vulnerability windows extend year-round for harbour and harp seals, in spring-summer-fall for grey seals, and in winter-spring for hooded seals. Vulnerability windows to birds run from river exit to the time when post-smolts are too large to eat.

Despite large sampling effort, salmon remains have been found in only two harp seal stomachs, two grey seal stomachs, one harbour seal stomach, and one common murre stomach in the Northwest Atlantic. Four other records from grey seals may reflect fish stolen from nets.

Potential impact of seal and seabird predation on marine-phase salmon was modeled under scenarios where predators took given percentages of prey biomass. If all seal and seabird predators combined remove 100% of a post-smolt cohort, the post-smolts would constitute 0.04% of their diet. The predator with the largest consumption is the harp seal. If harp seals take 100% of a post-smolt cohort, then post-smolts would be 0.09% of their diet.

Seals and seabirds in the Northwest Atlantic could harvest a high percentage of marine-phase salmon, even though salmon is a rare item in their diets. Given the rising populations of seals and some seabirds it is plausible that seal and seabird predation could have caused the decline in pre-fishery salmon numbers. However, present data are insufficient to determine whether this in fact occurred.

RÉSUMÉ

Ce document cherche à déterminer si la prédation par les phoques et par les oiseaux marins aurait pu causer le déclin majeur dans l'abondance pré-pêche du saumon de l'Atlantique Nord-Américain. Le taux de croissance du saumon durant sa phase marine était modélisé comme une série de courbes logistiques. Le nombre des saumons vivants étaient modélisé à l'aide d'une fonction de mortalité basée sur la taille corporelle, les estimés des saumoneaux qui sortaient des rivières, et l'abondance des adultes avant la pêche. La biomasse estimée des post-saumoneaux durant les années 1990 a augmenté de façon marquée durant l'été pour atteindre un maximum de 1,400-1,800 t tard en automne.

Les fenêtres de vulnérabilité à la prédation étaient considérées comme étant les périodes durant lesquelles les saumons étaient dans la même place que les phoques ou les oiseaux marins, et les saumons avaient une taille convenable aux prédateurs. Tous les phoques et tous les oiseaux marins considérés dans cette analyse consomment les proies de la taille d'un saumoneau. Les phoques consomment les saumons en phase marine de toute taille, mais les oiseaux marins sont limités aux petites proies, et les post-saumoneaux deviennent trop gros pour eux entre le mi-juin et l'automne, dépendant de l'espèce d'oiseau. Les fenêtres de vulnérabilité sont ouvertes à l'année longue pour les phoques communs et les phoques de Groenland. Elles sont ouvertes en printemps-été-automne pour les phoques gris et en hiver-printemps pour les phoques à capuchon. Les fenêtres de vulnérabilité aux oiseaux s'étendent de la sortie des rivières jusqu'au moment où les poissons sont trop gros à manger.

Malgré un grand effort d'échantillonage, les restants des saumons ont été trouvés seulement dans deux estomacs du phoque de Groenland, deux estomacs du phoque gris, un estomac du phoque commun, et un estomac d'une marmette commune dans le nord-ouest de l'Atlantique. Quatre autres records provenant des phoques gris auraient pu être originaires des poissons volés des filets.

L'impact potentiel de la prédation des phoques et les oiseaux marins était modélisé dans les scénarios dans lesquelles les prédateurs consomment les certains pourcentages de la biomasse de la proie. Si les phoques et les oiseaux marins enlèvent 100% d'une cohorte de post-saumoneaux, les post-saumoneaux constitueraient 0.04% de la diète des prédateurs. Le prédateur avec la plus grande consommation est le phoque de Groenland. Si ce prédateur consomme 100% d'une cohorte des post-saumoneaux, les post-saumoneaux seraient 0.09% de leur diète.

Les phoques et les oiseaux marins du nord-ouest de l'Atlantique pourraient récolter un fort pourcentage des saumons en phase marine, même si le saumon est rare dans leurs diètes. Étant donné que la population des phoques et de certaines espèces d'oiseaux marins sont en état de croissance, il est plausible que la prédation par les phoques et par les oiseaux marins aurait pu causer le déclin des saumons au stade pré-pêche. Pourtant, l'information présentement disponible est insuffisante pour déterminer si ceci est le cas.

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INTRODUCTION

Pre-fishery abundance of Atlantic salmon of North American origin has declined two-fold or more since the early 1980s (Anon. 1999a, Marshall et al. 1999). At the same time, densities of juvenile salmon in many major rivers have remained strong, and in some cases increased. This suggests that the increased mortality occurs either during the pre-smolt winter, or (more likely) during the salmon's estuarine or marine phases.

Dempson et al. (1998) reviewed legal and illegal fisheries, marine environmental conditions, disease, parasites, and predation as possible causes of the decline. No evidence was found to clearly link any of these factors to the salmon decline. However, it was noted that the decrease in salmon returns has coincided with major changes in the physical and biological environment of the Northwest Atlantic. Such changes when acting at the ecosystem level may be termed "regime shifts," which are commonly followed by declines in the productivity of some species and increases in others (Steele 1996).

One of these changes is an increase in numbers of seals and certain species of seabirds. A few dietary studies of seabirds and seals in eastern Canadian waters have reported salmon in small, usually trace, amounts, but most have reported no salmon at all. This suggests that salmon is of inconsequential importance to these predators. However, it does not necessarily follow that the predators are of inconsequential importance to salmon.

The main purpose of this paper is to determine whether seal and seabird predation could be of sufficient magnitude to cause, or be a major contributor to, the decline of North American Atlantic salmon returns. It must be emphasized that the paper is an examination of plausibility only, because current data are insufficient to determine whether seals and seabirds are causative agents in the salmon decline.

To achieve this purpose we a) estimate the numbers and biomass of post-smolt salmon in the sea, b) determine times and locations of salmon vulnerability to seal and seabird predation, c) review available records of salmon predation by seals and seabirds, and d) determine whether current dietary sampling programs are adequate to measure salmon predation by seals and seabirds. We also identify research endeavors likely to shed light on the effect of seal and seabird predation on salmon populations.

Due to their particular mode of feeding, northern gannets appear to have the highest likelihood of any seal or seabird species of capturing salmon. Potential effects of gannet predation on salmon are evaluated separately (W.A. Montevecchi unpubl.). In the present paper, seabirds are taken to include species whose foraging habitat includes the offshore zone. This excludes great and double-crested cormorants, which are exclusively inshore and estuarine in their marine distribution. The post-smolt stage of Atlantic salmon refers to the period between river exit and 31 December of the same year.

DISTRIBUTION, GROWTH, AND BIOMASS OF SALMON AT SEA

Marine migrations of North American Atlantic salmon

With the exception of salmon from inner Bay of Fundy rivers which complete their life cycle in the Fundy-Gulf of Maine region, salmon from west Atlantic rivers appear as 1 sea winter adults in the general area of the Labrador Sea (Reddin 1988, Ritter 1989). Our understanding of post-smolt movements between home rivers and the Labrador Sea is based on limited information from research fishing in the northwestern Gulf of St. Lawrence and the Labrador Sea, returns of tags from commercial fishers, and from predation records (Allen et al. 1972, Reddin 1988).

Ritter (1989) compiled post-smolt tag returns from Quebec, Maritime, and New England rivers by month and capture location. There were 306 recoveries of tags applied to smolts in the Saint John River and rivers in Maine (Table 1) (recoveries with unknown recapture dates are excluded). Most (283, 92.5%) of these occurred in the Atlantic coast south of the Gulf of St. Lawrence. Twenty-one (6.7%) came from Labrador and the Atlantic coast of Newfoundland, and two (0.7%) came from the west coast of Newfoundland. Recoveries from south of the Gulf (Atlantic coast of Nova Scotia, Bay of Fundy, Gulf of Maine) were reported in June to October, and recoveries in the Gulf and north were reported in June to September. In all zones (south of Gulf, Gulf, north of Gulf) more than 50% of recoveries were reported in July.

More than half (42 of 77) of recoveries of tags applied to smolts in Southwest Nova Scotia rivers occurred in the mouths of home rivers (Table 1). Of the remaining 35 recoveries, 27 (77.1%) occurred in Fundy or Atlantic Nova Scotia waters. Four (11.4%) came from the northeast and south coasts Newfoundland, two from Labrador (5.7%), and two (5.7%) came from the Lower North Shore of the Gulf of St. Lawrence. Nova Scotia recoveries were reported from June to September, with a peak in June. All Newfoundland and Gulf recoveries were in July, and the Labrador recoveries were in August and September.

About half (19 of 37) of tag recoveries for post-smolts in the Gulf of St. Lawrence came from home river mouths (Table 1). Of the remaining 18, 11 (55.0%) came from within the Gulf, two (10.0%) came from the east side of Cape Breton Island, one (5.0%) came from the Southern Shore of the Avalon Peninsula, one (5.0%) came from the east side of the Great Northern Peninsula, and three (15%) came from southern Labrador. Gulf recoveries were reported in June to October, Cape Breton and Newfoundland recoveries were reported in June-July, and in Labrador recoveries in August-September (Ritter 1989).

On the basis of tag recoveries at seabird colonies on the Avalon Peninsula and the northeast coast of Newfoundland, Montevecchi et al. (1988) suggested that post-smolts from the Atlantic coast south of the Gulf of St. Lawrence migrate to the Labrador Sea by passing east of Newfoundland. However, the presence of post-smolts from the Saint John and the LaHave rivers in the

northeastern Gulf (Ritter 1989) suggests that a route to the west of Newfoundland may also be used.

Caron's (1983) tagging analysis suggests that post-smolts from the northwest Gulf of St. Lawrence migrate from west to east across the northern Gulf during the post-smolt summer, which implies that these fish will leave the Gulf through the Strait of Belle Isle. One tag applied in the Miramichi was recovered on the east side of the Great Northern Peninsula in July (Ritter 1989), which implies a similar route. A tag from the Gaspé Peninsula was recovered on the Southern Shore of the Avalon Peninsula in June or July, and a tag applied on the Margaree was found off eastern Cape Breton in June. These recoveries imply a route through Cabot Strait.

Research fishing with surface-set gillnets in 1987, 1988, 1991, and 1998 established that post-smolts are present in substantial numbers in September-October in the Labrador Sea, especially in the area between 56° and 58° (Reddin and Short 1991, Reddin unpubl. data). These fish include a wide range of river ages, which implies that post-smolts from a broad geographic area of North America are represented.

Post-smolts were also found in commercial and research fishing in inshore waters in the Baie Trinité-Sept-Îles area of the northwestern Gulf in August-October 1982-1985 (Dutil and Coutu 1988). Because sampling occurred in only a very small area compared with Labrador Sea studies, no comparison can be made regarding the relative sizes of post-smolt populations occupying the Gulf and the Labrador Sea.

Reddin and Short (1991) suggested that post-smolts winter in the Labrador Sea, based on their presence there before and after winter, and the availability of water of suitable temperature. In their second summer at sea, fish destined to return as 2SW adults tend to move to the northern Labrador Sea and off the west coast of Greenland, although some remain in coastal Newfoundland waters (Reddin 1988). Fish which will mature as 1SW adults do not undertake this migration, and instead return to their natal rivers. Non-maturing adults return from Greenland in fall via the Labrador coast, and form concentrations in an area east of the Strait of Belle Isle. Further concentrations are found in the subsequent spring in the area east of the Grand Banks, suggesting that non-maturing 1SW adults winter in the general area of the Southern Labrador Sea and the northern Grand Banks (Reddin 1988).

Migratory patterns of adult Atlantic salmon are reasonably well known (except during winter) because of the history of directed commercial fishing. However, knowledge of post-smolt movements is sketchy at best. Tagging results are based on bycatch of commercial fisheries, which depend on the presence of gear capable of capturing post-smolts. Use of such gear is likely to vary seasonally and geographically. Return rates will also be affected by the increasing size of post-smolts, which determines their susceptibility to capture in a particular gear, and by the decreasing number of post-smolts due to natural mortality.

Because of these biases, available data cannot be used as a quantitative indicator of post-smolt migrations. Nevertheless, several points emerge from the tagging data compiled by Ritter (1989): 1) In all cases, the majority of post-smolt tag reports came from the region where the tag was applied and records from Newfoundland and Labrador accounted for a small portion of the total. This suggests that substantial numbers of post-smolts do not migrate out of their home region before fall. 2) Post-smolt migrations are diffuse in space and time. Tag records show no orderly progression of increasing distance from home region with time; instead peaks of recaptures occur simultaneously in local and distant (Newfoundland) waters. This suggests that some post-smolts migrate to the Labrador Sea soon after river exit while others remain in the region of their home river. 3) Migratory routes vary among post-smolts originating within the same river or region. Some Gulf post-smolts appear to use the Cabot Strait as a migratory route and some post-smolts from south of the Gulf appear to use the Strait of Belle Isle.

The records reviewed herein confirm the presence of post-smolts at certain times and places, but due to incomplete sampling, cannot confirm absence from other areas. Directed research fishing has been conducted only in the southern Labrador Sea and in the northwestern Gulf. Without similar efforts in other areas, the possibility that post-smolts form concentrations elsewhere cannot be excluded. Tagging records indicate that at least some post-smolts from Gulf of Maine, Scotian Shelf, and Gulf of St. Lawrence rivers spend summer and perhaps fall in their home regions. Whether these fish migrate to the Labrador Sea and winter there, or remain in their home regions and find deep-water wintering sites with suitable temperatures, is unknown.

For the purpose of determining windows of predation vulnerability, it is assumed that post-smolt salmon occupy the Fundy-Gulf of Maine area, the Scotian Shelf, the Gulf of St. Lawrence, banks around Newfoundland, and the Labrador Sea during their post-smolt summer. It is further assumed that all post-smolts (other than inner Bay of Fundy populations) migrate to the Labrador Sea by 31 October, and winter there.

Growth rates of salmon at sea

Marine-phase growth of Atlantic salmon was modeled with a series of logistic curves, with the ascendant portion of the combined curve representing summer growth and the asymptotic portion representing winter growth quiescence (Figs. 1-4). Curves were fitted to the following anchor points:

Date	Sea age (d)	Fork length (cm)	Weight (g)
1 Jun	0	13.75	20.8
9 Aug	70	23.4	195.9
1 Oct	123	36.4	555
1 Jul	395	52.5	1,580
1 Jul	760	73.4	4,430

The logistic equations (Pitcher and Hart 1982) are:

$$L_t = C + \frac{L_\infty}{1 + e^{-g(t-t_0)}}$$

for length and

$$W_t = C + \frac{W_\infty}{1 + e^{-g(t-t_0)}}$$

for weight.

For length (cm), equation parameters are:

Stanza	Sea age (d)	C	L_∞	g	t_0
1	0-272	11.73	32.78	0.031	86.8
2	273-636	43.7	25	0.024	149
3	>636	68.4	80	0.026	230

For weight (g), equation parameters are:

Stanza	Sea age (d)	C	W_∞	g	t_0
1	0-272	-10.4	1146	0.0286	124.86
2	273-636	1105	2750	0.029	177
3	>636	3830	5000	0.029	193

River exit date was taken as 1 June. River exit measurements were taken in the Miramichi by Allen et al. (1972) (lengths) and by R.A. Cunjak, University of New Brunswick, unpubl. (weights). Measurements for August were made on 21 post-smolts recovered from a northern gannet colony on Funk Island, off the northeast coast of Newfoundland, on a mean date of 9 August (W.A. Montevecchi unpubl.). Length measurements (cm) were converted to weight (g) by the equation $0.1807*\text{length}^{2.213}$, which was derived from measurements of post-smolts captured in fall research cruises in the Labrador Sea. Measurements for October were the means of lengths and weights recorded in these cruises (n=375). Measurements for sea ages 395 and 760 d were from virgin 1SW and 2SW salmon returning to the Miramichi River (Moore et al. 1995).

Growth curves fitted in this way were similar to those based on post-smolt records from the Bay of Fundy (Allen et al. 1972) (Fig. 1). However, plotted growth was much higher than growth reported for post-smolts in the northwestern Gulf of St. Lawrence by Dutil and Coutu (1988) (Figs. 1 and 3). In mid-August, the two curves differed by a small margin, but by October Labrador Sea post-smolts were nearly double the weight of those from the northwestern Gulf.

Numbers and biomass of post-smolt salmon

Estimating numbers of post-smolts alive through time requires knowledge of the initial population, the final population, and a function that calculates mortality. Numbers of smolts leaving North American rivers in 1977-1996 were estimated as follows. Percentages of exiting wild smolts that return as 1SW adults are available for 10 Canadian rivers (Table 2). Not all rivers have data for the full time series, and some rivers may have higher return rates than others. This means that biases could be introduced if return rates for each year were simply the raw means of available data. Correction factors for missing years were calculated by dividing the mean of directly measured return rates for the site by the mean return rate for other sites for the same years (Table 2). Missing return rates were estimated as the product of the correction factor and the mean of available return rates in the same year.

Return rates could be subject to an additional bias because the proportion of salmon returning after various sea ages varies regionally. This means that a region with a high proportion of multiple sea winter returnees is likely to have a lower rate of 1SW returns than a region with few MSW returnees. To avoid this bias, return rates were weighted by the ratio of the proportion of returnees coming at 1SW for individual rivers, to the overall proportion of 1SW returnees among the North American returning salmon population (Table 2). Overall return rates to 1SW were taken as the mean of these weighted return rates.

Number of salmon returning to North American rivers at age 1SW was taken from ICES compilations (Anon. 1999a). The North American smolt run was estimated by dividing 1SW returns by the smolt to 1SW return rate (Table 3).

Number of salmon alive on 1 July in their 1SW year was taken as the sum of ICES estimates of pre-fishery maturing and pre-fishery non-maturing 1SW fish (Anon. 1999a) (Table 3).

Natural mortality of fishes is strongly influenced by size, with large fish suffering lower mortality rates than small ones (Doubleday et al. 1979, McGurk 1986, Anderson 1988, Mangel 1994). Numbers of salmon alive between river exit and 1 July in the 1SW year were modeled with Lorenzen's (1996) weight-based mortality function: $M_W = M_u W^b$, where M_W is instantaneous mortality at weight, M_u is natural mortality at unit weight, and b is the allometric scaling factor. Using literature values for ocean fish, Lorenzen (1996) calculated M_u as 3.69 and b as -0.305, with mortalities annual and weights in grams. For each cohort, numbers of salmon alive were calculated for each day between river exit and 1 July of the 1SW year, using the estimated North American smolt run as a starting point. Daily mortalities were calculated by the Lorenzen equation, using modeled weights (Fig. 4), the allometric exponent for ocean fish, and an arbitrary value of M_u. Populations alive each day were reduced by the mortality calculated for the previous day. The actual mortality schedule and number alive were estimated by iteratively varying M_u (using Microsoft Excel's Goal Seek function) until the final population matched the estimated prefishery abundance for 1SW fish.

Post-smolts commonly encounter high levels of predation when they enter estuaries; osmotic stress may exacerbate their vulnerability to capture (Larsson 1985, Hislop and Shelton 1993). Mortality and number alive were modeled for scenarios with no mortality upon river exit, with 20% mortality upon river exit, and with 40% mortality upon river exit.

In all three scenarios, estimated daily mortalities and number alive declined steeply in the post-smolt summer,

as the fish rapidly gained weight (Table 4, Figs. 5-6). Calculations based on averaged values for 1990-1996 indicate a late fall population of about 2,000,000 (Fig. 6). Mortality leveled off during the period of slow growth in the winter, but numbers continued to decline during this period, albeit much less rapidly than during the post-smolt summer. Initially, numbers of post-smolts alive diverged broadly among the three scenarios of river exit mortality, but by late fall these differences had been largely erased. This is due to the stabilizing effect of the final population, which was held constant in all scenarios.

Biomass was calculated as the product of number alive and daily weight at age. Based on averaged values for 1990-1996, biomass in the three scenarios rose from about 200 t at river exit to about 1,400-1,800 t in late fall (Table 5, Fig. 7). Biomass declined over winter because of minimal growth and continuing mortality.

WINDOWS OF VULNERABILITY TO SEAL AND SEABIRD PREDATION

Predation can take place only if the prey is within the size range taken by the predator, and the predator and prey co-occur in time and space. Acceptable prey size ranges can be deduced from examination of prey taken by predators. Lengths of prey taken by seals and seabirds are typically calculated from otoliths found in predator stomachs. Minimum prey sizes based on otolith dimensions were 3-7 cm for grey seals, 5-10 cm for harbour seals, 2 cm for harp seals, and 13.4 cm for hooded seals (Table 6, see also Anon. 1999c). These sizes are smaller than smolts at the time of sea exit, which indicates that smolts are within the size range taken by these predators. Maximum reported prey sizes, based on otolith examination, were 79.7 cm for grey seals, 50-55 cm for harbour seals, 57 cm for harp seals, and 48.1 cm for hooded seals (Table 6). The otolith method of calculating prey size selection assumes that the predator will consume the entire fish, including the head. If heads are discarded, the method will underestimate the maximum size of acceptable prey. Boulva and McLaren (1979) observed harbour seals eating large fish in pieces at the surface. On the basis of the low number of otoliths found, they concluded that heads were often left uneaten. In Scotland, grey and harbour seals often eat salmon in pieces, leaving the head and much of the skeletal material (Pierce et al. 1991a, 1991b, 1997; Shearer 1992). However most Scottish reports of seal predation on salmon appear to refer to consumption of net-caught fish (Boyle et al. 1990). On 30 April 1984, Reddin (unpubl. data) observed a harbour seal eating an adult salmon in Aberdeen Harbour, Scotland. Only the soft parts were consumed and the head and backbone were discarded.

Heads of large fish are not always rejected. Grey seals on Anticosti took cod up to 79.7 cm, estimated from otolith length (Table 6), and captive grey seals feeding on adult salmon have been observed to consume the head (Pierce et al. 1997). Pemberton et al. (1994) reported that harp seals feeding on cod (mean length 49 cm) spilling from a trawl swallowed them headfirst and whole. They also reported observations of captive harp seals holding large cod (length not given) in their foreflippers and eating them, beginning with the belly. Fragments which fell away were recovered and the entire fish was eaten.

On the basis of these observations, it appears that adult salmon fall within the size range taken by harbour, grey, and harp seals. We have located no reports of visual observations of hooded seals eating large fish, but on the basis of the hooded seal's large size, it seems likely that they would do so.

Minimum prey sizes of northern fulmars, black-legged kittiwakes, herring gulls, glaucous gulls, common murres, and thick-billed murres are much lower than smolt size (Table 7). Minimum prey size reported for great black-backed gulls was 19 cm, which is larger than smolt size (Table 7). However in this study fish of smolt size were unavailable. Given the omnivorous habits of gulls, it is likely that all seabirds considered in this paper consume smolt-size fishes.

Maximum prey sizes for seabirds are much lower than those of seals (Table 7). Live prey taken by northern fulmars was consistently smaller than 17 cm in several studies, but the single study in which trawl samples were available indicated this was the maximum size locally available. Hence the true upper limit of live prey size could be larger than this. Fulmars are capable of swallowing much larger items; birds scavenging on fishery discards took fish up to 30 cm long. This is a major increase over maximum sizes in live prey studies, but it is possible that fulmars can handle large prey only when it is dead. Greater shearwaters have been found to take fish and squid up to 20 cm. It is presumed that sooty shearwaters have a similar size selection. Black-legged kittiwakes have been found to take prey up to 16 cm. Herring gulls and great black-backed gulls take prey up to 30 and 39 cm respectively. Maximum prey size of glaucous gulls is only 13.5 cm, but available prey were no bigger than this. Based on their size, it is likely that they can take much larger prey, perhaps of the range of herring gulls. Common murres take prey up to 17 cm and thick-billed murres take prey up to 19 cm.

Size limits noted above were converted into dates on the basis of calculated weight at sea age (Figs. 1 and 2).

Marine distributions of seal and seabird species are reported by Hammill and Stenson (1997) and Diamond et al. (1993), respectively. Although grey seals are increasingly being reported in Labrador, they are common and widespread only in the Gulf of St. Lawrence and in the Atlantic south of the Gulf. Post-smolts are assumed to vacate this area in the winter. Hence grey seals produced a split vulnerability window, with predation potentially occurring in the post-smolt summer and fall, and in the following year when 1SW fish return toward natal rivers in the Gulf and Maritimes (Table 8). Harbour seals are resident in the Gulf, the Maritimes, and Newfoundland, and hence co-occur with salmon throughout the year. Their vulnerability window therefore includes their entire marine phase. Most harp seals move south from the Arctic in fall and early winter, occupying Gulf and Newfoundland waters until spring when they return north. However, 5% of harp seals are thought to

remain in southern waters year-round (Hammill and Stenson 1997). Thus the salmon vulnerability window to harp seal predation includes the entire marine phase. Hooded seals are in southern waters from late fall to spring. Their vulnerability window therefore runs from December of the post-smolt year to May of the 1SW year.

Because of their smaller prey size limits, birds can prey on salmon only during the post-smolt year (Table 8). Post-smolts out-grow the size limits of kittiwakes in June, and the size limits of fulmars, common murres, and shearwaters in July. Salmon do not have a vulnerability window to thick-billed murres because this species is on its northern breeding grounds at the time when salmon are small enough to be taken. Herring and great-blacked backed gulls can take larger food than the other seabird species, and can prey on post-smolts into the fall.

RECORDS OF SALMON PREDATION BY SEALS AND SEABIRDS

We have located 10 records of Atlantic salmon predation from seal and seabird stomachs in eastern Canada (Table 9). Four of these occurred in the Miramichi estuary from 1950 to 1970. Seals commonly rob salmon from gillnets (Rae and Shearer 1965, Reddin and Felt 1998), so it is uncertain whether the Miramichi records represent wild-caught fish. There are two records of grey seal predation on salmon that cannot be explained by net-stealing. One is from the Magdalen Islands and the other is from Anticosti Island where otoliths from six salmon were found in one stomach. A tag that had been applied to a smolt was found in a harbour seal stomach in the Bay of Fundy. Salmon remains were found in two harp seal stomachs, one in the St. Lawrence estuary and one on the northeast coast of Newfoundland. Finally, a tag was found in a common murre stomach from eastern Newfoundland.

In addition to the 10 records noted above, Comeau (1909) reported finding salmon in a harp seal stomach, and stated that grey seals raid salmon nets.

Lengths of salmon were estimated from otoliths removed from three predator stomachs (Table 9). In all cases the calculated lengths were smaller than the size range expected at that time of the year (although the largest Anticosti size might be a small grilse). This suggests that either a) inappropriate otolith-length relations were used, b) erosion of the otoliths biased the length calculations, or c) otoliths came from a species other than Atlantic salmon. Tollit et al. (1997) showed that erosion of otoliths substantially altered the relation between otolith size and fish size, and required the use of correction factors ranging from 9 to 30% for otoliths of medium digestion grade.

The report of harp seal predation in the St. Lawrence estuary came at an unexpected time (mid-April), which casts some uncertainty on the record.

Two of the records were based on personal communications, and were not mentioned in the papers that presented the dietary studies that obtained the records (Bowen and Harrison 1996, Piatt 1987). In both cases (harbour seal in Fundy, murre in Newfoundland) the artifact found was a salmon tag, leaving no doubt as to prey identity. This suggests that diet investigators may not necessarily report prey that is unusual, or does not match the format in which other data are presented (i.e. a tag would not readily fit in a table reporting otolith records).

In addition to stomach analysis, evidence for seal predation is available from six sight records of seals pursuing, holding, or eating salmonids in Newfoundland and Labrador (Table 10). Two of the Newfoundland/ Labrador records occurred in areas where commercial fishing was permitted, leading to the possibility that the salmon observed in the seal's mouth was stolen from a net. In the remaining four cases there were no fishing nets in the vicinity; hence these observations can be taken as valid records of predation on free-swimming fish. Two of the records involved adult salmon and one involved a juvenile salmonid (either trout or salmon). One record was of a seal pursuing an adult salmon into a trap. Three observations came from rivers and estuaries in Labrador, where seal presence commonly coincides with salmonid runs.

Diet studies provide good temporal and spatial coverage for grey and harp seals in eastern Canada (Table 11), although some significant gaps remain (Hammill and Stenson 1997). Coverage is less extensive for harbour and hooded seals. Published diet investigations have not been designed to measure salmon predation, and no study has targeted the estuaries of major salmon rivers where seals might prey on exiting smolts and kelts or returning adults.

Some papers explicitly report only major prey species, and ignore the rare ones like Atlantic salmon (Table 11). Sample size of food-containing grey seal stomachs totaled 1,315, although sample sizes are difficult to sum with certainty because some papers incorporate data from previous studies (Table 11). Of these, 1,094 samples were reported in papers which indicated that all prey were reported. Sample size of harbour seal stomachs is 659. All papers indicate full data disclosure, although the tag found in a stomach (Table 9) was not reported. Published reports of harp seal stomachs containing food total 3,145 (2,083 with full identification), but this figure is uncertain due to authors' inclusion of previous works. Sample size of food-containing harp stomachs in DFO files, including unpublished records, currently total about 6,100 (G. Stenson, DFO, pers. comm., April 1999).

Most diet studies of seabirds are conducted in the summer, which is advantageous from a salmon research point of view because that is when salmon are small enough for birds to eat. Nevertheless spatial coverage is poor for all species. The largest sample size is for common murres (Table 12) (N=4,778). The species with the poorest coverage are the shearwaters, which have not been sampled since 1978, and the fulmar, which has not been sampled at all in eastern Canada (Hatch and Nettleship 1998). No seabird diet studies have focused on the areas around the mouths of salmon rivers.

SEAL AND SEABIRD HARVEST IN RELATION TO SALMON BIOMASS

Hammill and Stenson (1997) estimated that grey, harbour, harp, and hooded seals consume 3.8 million t of food annually in eastern Canadian waters south of mid-Labrador. Eighty-two percent of this (3.1 million t) is due to harp seals (Table 13).

Seabird harvest has been estimated as 707,284 t for NAFO area 2J3KLNO, which runs from the mid-Labrador coast to the southern Grand Banks (Anon. 1999b), and as 80,102 and 108,419 t in the Gulf of St. Lawrence (locally breeding population only; Cairns et al. 1991 and Anon. 1999b, respectively). Total seabird harvest in eastern Canadian waters has not been estimated. However, Diamond et al. (1993) estimated seabird energy demand for eastern Canadian waters south of 60°N, and tabulated this demand by time period, geographical area, and predator species (or group of species). Diamond et al. (1993) noted that their energy demands for the "Labrador Sea" (from the edge of the continental shelf east to 45°W and north to 60°N) are likely overestimated because their data set oversampled the area near the continental shelf where birds tend to congregate. To compensate, we reduced energy demand in this area by 50%. We converted Diamond et al.'s (1993) energy demands into harvest tonnage by assuming an energy density of 5.1 kJ/g wet weight (Cairns 1998). This yields a total annual seabird harvest of 2.4 million t south of 60°N (Table 14).

Prey harvest by seals and seabirds was calculated for salmon vulnerability windows by summing harvest within the time period of vulnerability and for the geographic areas where salmon and the predator coincided (Table 13), using the harvest figures of Hammill and Stenson (1997) for seals and the re-analysis of Diamond et al.'s (1993) data (Table 14) for birds. Mean salmon biomass was then calculated for these periods of vulnerability, based on 1990-1996 data and assuming a 20% mortality on river exit (Table 5).

Percent of salmon in predator diet was calculated for scenarios in which the predator consumes 1%, 10%, and 100% of the salmon cohort. For seals, predation of post-smolts (prior to 1 January) and 1SW fish (after 1 January) was analysed separately. When the predator was assumed to consume 1% of the salmon cohort, salmon occupied 0.16% to 0.31% of the diet of harbour seals (Table 13). For all other species, salmon occupied less than 0.05% of diet during windows of salmon vulnerability. Under this scenario, post-smolts contributed 0.0009% and 1SW salmon contributed 0.0003% to harp seal diet. For species other than harbour and harp seals, salmon as a percentage of total prey ranged from 0.038% (black-legged kittiwakes) to 0.0026% (common murres).

Scenarios in which predators consumed 10% and 100% of salmon cohorts gave results which varied by one and two orders of magnitude, respectively, from those of the 1% consumption scenario. If harp seals consume 10% of the post-smolt population, then salmon will be 0.009% of diet. If harp seals consume 100% of post-smolts, then salmon will be 0.09% of diet. If harp seals consume 10% or 100% of 1SW salmon, then salmon will constitute 0.003% and 0.03% of prey, respectively.

Taking seal and seabird predators as a whole, and assuming that predation removes 1% of the salmon cohort, salmon would be 0.0004% of prey (Table 13).

Predator harvest of Atlantic salmon was estimated on the basis of the five records of seal and seabird predation since 1980 (Table 9). Salmon as a percent of total annual diet was estimated as numbers of salmon per stomach divided by the mean number of fish prey per stomach, all divided by the number of fully identified prey samples available for the predator in eastern Canadian waters (Table 15). These calculations are based on frequency of occurrence. Salmon contribution to harp seal diet at Les Escoumins (Beck et al. 1993) was available as percent by mass. Salmon as a percent of diet from this record was added to the salmon percent of diet value from the other harp seal predation record (from Brighton, Newfoundland).

Estimates of salmon as a percent of diet ranged from 0.0034% for harp seals to 0.389% for grey seals (Table 15). Application of these percents to total annual consumption of all prey species yielded salmon harvest estimates of 1,090 t for grey seals, 1.3 t for harbour seals, 106 t for harp seals, and 67 t for common murres. Comparison of these estimated harvests to salmon biomass during their windows of vulnerability indicated that grey, harbour, and harp seals and common murres eat 117, 0.1, 10.3, and 26.1%, respectively, of salmon biomass.

Hammill and Stenson (1997) estimated salmon predation by seals as part of their food consumption model. According to their model, grey seals consume 712 t of salmon (76% of biomass), and harp seals consume 2,474 t of salmon (240% of biomass).

DISCUSSION

Limitations to reliability

This study uses inference and results of energetics modeling to evaluate predation potential of seals and seabirds on salmon. The analysis is subject to errors and biases which may inflate, deflate, or alter in unpredictable directions the likely importance of seal and seabird predation to salmon. Major sources of error follow.

Factors which may lead to an overestimate seal and seabird impact on salmon:

a) Misidentification as salmon - For all three otolith records in seal stomachs, calculated lengths were unexpectedly small for the time of the year. This could mean that the otoliths were from species other than salmon (possibly sea trout). Alternatively, lengths may have been underestimated due to otolith erosion (salmonid otoliths are friable and erode readily; Boyle et al. 1990; see also Tollit et al. 1997).

b) Long retention of tags - Two of the records (harbour seal and common murre) were of tags. If tags are retained in stomachs longer than otoliths, then percent salmon in diet would be upwardly biased.

c) Predation risk altered by tags - Tags may increase the visibility of prey or impair its escape response, leading to increased vulnerability to predation. If the fish bearing the tags which were discovered in the harbour seal and murre stomachs were captured because they bore tags, then the percent of salmon in diet would be upwardly biased.

Factors which may lead to an underestimate of seal and seabird impact on salmon:

a) Incomplete reporting - Some studies note that only major prey species are reported. Studies that do not mention this may nevertheless also not present some data, given that two of the five post-1980 records are from personal communications, and were not mentioned in the diet studies that published other results. If some studies indicate that all results are reported but in fact they are not, then sample size will be inflated above its true value and harvests will be underestimated.

b) Failure to identify - Those assigned to stomach examination are more likely to accurately identify prey items which are common, even when they are in poor condition, than those that are rarely seen. Thus salmon otoliths, especially those in poor condition, might not be identified as such.

c) Missing heads - Seal predation on adult salmon will not be detected by otolith-based diet studies if heads are discarded, as has been observed in adult salmon and other large fish (Boulva and McLaren 1979, Pierce et al. 1991b, Reddin unpubl.).

Factors which lead to errors in either direction:

a) Sampling error - One or two records per predator is insufficient to reliably indicate percent salmon in predator diet.

b) Use of frequency of occurrence data - Counts of prey items accurately indicate proportion of diet only if the prey items are of similar size. This is unlikely to be the case.

c) Vulnerability windows to predators are calculated on the basis of simple length cut-offs. Instead, the actual upper size limit that predators can take is likely to be graduated (analogous to partial recruitment), with salmon progressively less vulnerable with increasing size. Cut-offs based on otolith analysis ignore possible delayed mortality due to predation attempts in which the salmon escapes, but subsequently dies of wounds.

d) Estimates of seal and seabird harvest generated by bioenergetics models are subject to substantial error (Shelton et al. 1997, Cairns and Kerekes in press).

Seals and seabirds as salmon predators

Despite the limitations noted above, there is sufficient bulk of evidence presented in this study to demonstrate that seals and seabirds are significant potential predators on North American Atlantic salmon during their marine phase. It is shown that post-smolt salmon are in a vulnerability window to seabird predation in the period following river exit, and that they are in the vulnerability window of at least one seal species during their full time at sea. Vulnerability may be greater in certain local situations, such as Labrador rivers that have year-round populations of harbour seals. Ability of salmon to flee predators in freshwater will be restricted by the size of the river and number of ponds and deep pools.

Records of salmon in seal and seabird stomachs are rare (only five records since 1980), indicating that salmon are at most a minute fraction of predator diet. However, biomass of salmon in the sea is very small; hence predation which is insignificant to the predator may be very important to the prey. On the basis of available diet data, salmon harvest as calculated in two analyses was greater than the total biomass available (Table 15). This result underlines the unreliability of estimating harvest on the basis of a handful of prey capture records. Nevertheless, it reinforces the suggestion that these predators could account for the majority of the salmon's total marine mortality. This review does not include predation by northern gannets, which have specialized feeding adaptations for medium-size fish which swim near the water surface, which allow them to harvest significant quantities of salmon (W.A. Montevecchi unpubl.).

Although large sample sizes have been amassed in diet studies of some predators, currently available diet data are inadequate to reliably assess salmon contribution to predator diet, which is a precursor to determining proportion of salmon biomass that is harvested. This situation is unlikely to change. Because salmon are relatively rare in the ocean, predators can harvest substantial fractions of salmon biomass even if salmon constitute minute fractions of predator diet. For harp seals preying on 1SW salmon, a harvest of 10% of biomass corresponds to salmon contributing 0.003% of seal diet. In this scenario, only one out of 33,490 prey items would be a salmon (provided that salmon are the same size as other prey). Sampling programs sufficiently large to accurately measure salmon contribution to predator diet would have to be huge, and beyond the realm of the possible. This means that we cannot rely on conventional diet sampling, even if it substantially increases, to clarify the effects of seal and seabird predation on salmon populations.

Although this study gives evidence that seals and seabirds could take substantial fractions of salmon populations in the marine environment, it does not necessarily follow that seal and seabird predation is the cause of the long-term decline in North American salmon returns. Even under normal circumstances (i.e. no population decline), the great majority of salmon that enter the sea die there. Therefore, for seal and seabird predation to have caused the decline, the rate of predation (percent of population removed) must have increased.

An increase in predation rate could occur as a result of rising predator numbers. Amiro (1998) showed that increasing harp seal populations in the Northwest Atlantic are statistically related to the decline in Atlantic salmon returns. Harp seals are the main predator among those considered in this paper, accounting for one half of the 6.2 million t of prey consumed by seals and seabirds in

eastern Canadian waters. Harp seal populations have been increasing at a rate of 4% annually (although they appear to have leveled off since 1996, Stenson et al. 1999). Populations of hooded seals have been increasing at 4.8%, and grey seal numbers have been rising at 12.6% at Sable Island and 6.8% in the Gulf of St. Lawrence (Hammill and Stenson 1997). Population levels of harbour seals are poorly known but appear to be rising. Numbers of murres and gannets are rising in eastern North America (Chardine et al. 1999). Population trends of seabirds which visit eastern Canadian waters as non-breeding migrants (fulmars, shearwaters) are unknown.

This study has emphasized what is plausible, because our present knowledge is insufficient to determine what is real. Its implicit assumption is that if there is more predation there will be fewer prey. However, the relation between marine predators and their prey is complex with many potential cause-and-effect chains, and predator increases do not necessarily lead to lower prey populations (Fiscus 1980, Gulland 1987, Butterworth 1992, Smith 1995).

This paper has examined the potential role of birds and seals as salmon predators, but has not considered cetaceans. Diets of most odontocete cetacean species have not been examined in the northwest Atlantic, but studies in the northeast Atlantic have reported that salmon are present in the diets of belugas and bottlenose dolphins (Anon. 1999c). Fontaine et al. (1994) found four salmonid otoliths in one harbour porpoise stomach from the Gulf of St. Lawrence system, but the otoliths were too eroded to identify the species. Size ranges of post-smolt salmon overlap the prey size distributions of most odontocete cetaceans (Anon. 1999c). Bioenergetics models estimate that cetaceans consume 1.9 million t annually in the Northeast Shelf of the United States and 6.3 million t annually in waters around Iceland (Kenney et al. 1997, Sigurjonsson and Vikingsson 1998). Estimates of harvest by cetaceans in eastern Canadian waters are unavailable, but are presumably substantial given the large harvests estimated for nearby waters. These points collectively suggest that cetaceans in eastern Canadian waters could be significant predators of Atlantic salmon.

FUTURE RESEARCH

Although the major problem with North American salmon populations appears to lie in the sea, most salmon research is directed toward fresh water. Conventional stomach analysis of seal and seabird predation in the open sea appears to have little potential to clarify the impact of marine predation on salmon because salmon predation is such a rare event. However, there are several lines of investigation that may increase basic understanding of the marine biology of Atlantic salmon, and which may ultimately assist in elucidating the predator-prey relations of salmon at sea. These include:

a) Fishermen's knowledge of post-smolts - Anecdotal reports from fishermen prompted Dutil and Coutu's (1988) work in the northwestern Gulf of St. Lawrence, which identified a gathering area for post-smolts. Fishermen's knowledge could be systematically polled to locate other areas where post-smolts are commonly bycaught.

b) Gannets as samplers - Samples obtained from gannets may be useful indicators of timing and routes of post-smolt migrations, and provide weights and measures and specimens for scale and otolith investigations (Friedland and Haas 1996). Gannets breed in six colonies in the Gulf of St. Lawrence and eastern and northeastern Newfoundland, and their diets can be readily and non-destructively sampled. Sampling from gannets is likely to produce data at lower cost than directed research cruises.

c) Research fishing - Surveys using surface gillnets (Dutil and Coutu 1988, Reddin and Short 1991) or trawls could be conducted to locate concentrations of post-smolts and obtain samples.

d) Salmon scarring - Scars attributed to seals are commonly found on salmon returning to rivers (Baum 1997; D. Sutherland and D. Moore, DFO, pers. comm.) Such scars could be investigated to determine whether the predator can be identified from the pattern of scarring. Scales from the scar area could be examined to determine if the age of scar can be determined from scale patterns. Scarring rates could be monitored to determine regional and temporal patterns.

e) Predator diet studies - There may be scope for better identification of salmon remains by those involved in predator diet analysis. Reference salmon otoliths should be provided where needed, and the utility of identifying and reporting salmon remains should be emphasized.

f) Scale and otolith patterns - Scales and otoliths can provide valuable insights into marine history (Friedland and Haas 1996, Friedland et al. 1996); such investigations should continue with emphasis on integrating findings with other sources of information on salmon's marine life.

g) Studies in estuaries - Predation by seals and birds (notably cormorants and gulls) on outgoing smolts, and by seals on returning adults, has potential to impact salmon populations. Unlike the high seas where adequate samples are impractical, this predation is localized, meaning that focused efforts would have a reasonable chance of elucidating predator impacts.

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Table 1
Recoveries of tagged post-smolts from New England, Maritime, and Quebec rivers. Data from Ritter 1989. Records with unknown recovery dates are excluded.

Home region	Recovery Region	Month of recovery					
		Jun	Jul	Aug	Sep	Oct	Total
Maine, Saint John R.	Home river mouth						0
	Gulf of Maine, Fundy, Atlantic Nova Scotia	45	145	87	5	1	283
	Gulf of St. Lawrence		2				2
	Atlantic coast, Newfoundland	3	11	4	1		19
	Southern Labrador		1		1		2
	Total	48	159	91	7	1	306
Southwest Nova Scotia	Home river mouth	39	3				42
	Gulf of Maine, Fundy, Atlantic Nova Scotia	18	7	1	1		27
	Gulf of St. Lawrence		2				2
	Atlantic coast, Newfoundland		4				4
	Northern Labrador			1	1		2
	Total	57	16	2	2	0	77
Gulf of St. Lawrence	Home river mouth	17	1	1			19
	Gulf of Maine, Fundy, Atlantic Nova Scotia	1		1			2
	Gulf of St. Lawrence	2	3	3	2	1	11
	Atlantic coast, Newfoundland		2[a]				2
	Southern Labrador			1	2		3
	Total	20	6	6	4	1	37

[a]Recaptured in either June or July

Table 2
Return rates (percent) of wild smolts to 1 sea winter adults in North American rivers.

Smolt year	Quebec			New Brunswick	Newfoundland						Mean
	Bec-Scie	de la Trinité	Saint-Jean	Catamaran	High-lands	Camp-bellton	Western Arm Brook	Northeast Trepassy	Rocky River	Conne River	
Return rates[b]											
1977	(0.81)	(1.21)	(0.25)	(5.80)	(0.90)	(3.16)	3.10	(3.82)	(1.94)	(3.66)	2.47
1978	(3.14)	(4.68)	(0.97)	(22.47)	(3.49)	(12.22)	12.00	(14.80)	(7.50)	(14.16)	9.54
1979	(1.47)	(2.18)	(0.45)	(10.49)	(1.63)	(5.70)	5.60	(6.90)	(3.50)	(6.61)	4.45
1980	(0.78)	(1.17)	(0.24)	(5.62)	(0.87)	(3.05)	3.00	(3.70)	(1.88)	(3.54)	2.39
1981	(0.86)	(1.29)	(0.27)	(6.18)	(0.96)	(3.36)	3.30	(4.07)	(2.06)	(3.89)	2.62
1982	(2.38)	(3.55)	(0.74)	(17.04)	(2.65)	(9.27)	9.10	(11.22)	(5.69)	(10.74)	7.24
1983	(0.58)	(0.86)	(0.18)	(4.12)	(0.64)	(2.24)	2.20	(2.71)	(1.38)	(2.60)	1.75
1984	(0.75)	1.61	(0.25)	(5.91)	(1.00)	(3.51)	2.20	(3.46)	(1.97)	(3.34)	2.40
1985	(1.25)	2.43	(0.41)	(9.83)	(1.67)	(5.84)	3.90	(5.76)	(3.28)	(5.55)	3.99
1986	(1.33)	1.40	(0.43)	(10.17)	(1.70)	(5.94)	2.50	8.10	(3.40)	(5.73)	4.07
1987	(1.66)	2.19	(0.55)	(13.31)	(2.26)	(7.90)	2.10	6.90	(4.44)	10.20	5.15
1988	1.61	3.67	(0.46)	(10.83)	(1.88)	(6.57)	3.00	3.70	(3.62)	7.60	4.29
1989	1.68	2.57	0.55	(11.20)	(1.91)	(6.67)	3.80	4.20	(3.74)	7.30	4.36
1990	1.69	2.69	0.45	10.30	(1.59)	(5.57)	2.20	5.20	2.50	4.20	3.64
1991	1.17	1.56	0.49	11.10	(1.47)	(5.15)	3.60	2.60	3.10	3.40	3.36
1992	1.27	0.81	0.40	5.00	(1.37)	(4.80)	5.30	4.70	3.70	4.00	3.14
1993	0.92	0.67	0.35	13.60	1.45	9.05	6.80	5.40	3.10	2.70	4.40
1994	1.17	0.62	0.33	13.50	1.64	7.29	8.90	8.50	3.90	5.80	5.16
1995	1.40	0.92	0.57	8.50	1.64	8.08	8.10	9.20	4.60	7.20	5.02
1996	(0.94)	0.65	0.29	9.90	3.21	3.38	3.50	2.90	3.10	3.40	3.13
1997	(1.10)	1.66	(0.38)	5.50	1.40	5.30	7.50	5.00	2.40	2.90	3.31
Correction factors for missing values[c]											
1977-1983	0.26	0.39	0.08	1.87	0.29	1.02		1.23	0.63	1.18	
1984-1985	0.40		0.13	3.10	0.53	1.84		1.82	1.04	1.75	
1986	0.33		0.11	2.54	0.42	1.48			0.85	1.43	
1987	0.31		0.10	2.49	0.42	1.48			0.83		
1988			0.12	2.77	0.48	1.68			0.92		
1989				3.34	0.57	1.99			1.12		
1990-1992					0.44	1.52					
1996	0.26										
1997	0.26		0.10								
1SW returns as a proportion of total returns[d]											
	0.54	0.55	0.24	0.72	0.93	0.93	0.93	0.93	0.93	0.93	0.74
Ratio of river 1SW return proportion to North American 1SW return proportion											
	0.73	0.73	0.33	0.96	1.25	1.25	1.25	1.25	1.25	1.25	
Return rates weighted for proportion returning as 1SW[e]											
1977	1.11	1.65	0.77	6.03	0.72	2.52	2.48	3.05	1.55	2.92	2.28
1978	4.28	6.37	3.00	23.33	2.79	9.76	9.59	11.82	5.99	11.31	8.82
1979	2.00	2.97	1.40	10.89	1.30	4.56	4.47	5.52	2.80	5.28	4.12
1980	1.07	1.59	0.75	5.83	0.70	2.44	2.40	2.95	1.50	2.83	2.21
1981	1.18	1.75	0.82	6.41	0.77	2.68	2.64	3.25	1.65	3.11	2.43
1982	3.25	4.83	2.27	17.69	2.11	7.40	7.27	8.96	4.54	8.58	6.69
1983	0.78	1.17	0.55	4.28	0.51	1.79	1.76	2.17	1.10	2.07	1.62
1984	1.03	2.19	0.76	6.14	0.80	2.80	1.76	2.77	1.58	2.67	2.25
1985	1.71	3.31	1.27	10.21	1.33	4.66	3.12	4.60	2.62	4.44	3.73
1986	1.81	1.91	1.33	10.56	1.36	4.75	2.00	6.47	2.71	4.58	3.75
1987	2.26	2.98	1.69	13.82	1.80	6.31	1.68	5.51	3.55	8.15	4.78
1988	2.20	4.99	1.41	11.25	1.50	5.24	2.40	2.96	2.89	6.07	4.09
1989	2.29	3.50	1.70	11.63	1.52	5.33	3.04	3.36	2.99	5.83	4.12
1990	2.31	3.66	1.37	10.69	1.27	4.45	1.76	4.15	2.00	3.36	3.50
1991	1.60	2.12	1.51	11.52	1.17	4.11	2.88	2.08	2.48	2.72	3.22
1992	1.74	1.10	1.23	5.19	1.09	3.83	4.23	3.75	2.96	3.20	2.83
1993	1.25	0.92	1.06	14.12	1.16	7.23	5.43	4.31	2.48	2.16	4.01
1994	1.59	0.85	1.02	14.02	1.31	5.82	7.11	6.79	3.12	4.63	4.63
1995	1.91	1.26	1.75	8.82	1.31	6.45	6.47	7.35	3.67	5.75	4.47
1996	1.28	0.88	0.89	10.28	2.57	2.70	2.80	2.32	2.48	2.72	2.89
1997	1.50	2.25	1.16	5.71	1.12	4.23	5.99	3.99	1.92	2.32	3.02

Table 2 (continued)

[a]Data from Anon. 1999a, R.A. Cunjak in Chaput et al. 1999, and O'Connell et al. 1998.

[b]Unbracketed return rates are directly measured. Bracketed rates are estimated as the product of correction factors and the mean of available return rates in the same year. For example, the return rate for the Saint-Jean in 1984 is calculated as 0.13*(1.62+2.2)/2=0.25

[c]Correction factors are the mean of directly measured return rates for the site, divided by the mean of return rates for other sites for the same years. For example, the mean return rate for the Saint-Jean for 1989-1996 is 0.43%. The mean return rate for Trinité and Western Arm Brook for these years is 3.29%. The correction factor is 0.43/3.29=0.13.

[d]Data for Quebec for 1984-1995 (Caron 1996a and b); data for New Brunswick for 1977-1996 (Chaput et al. 1999); data for Newfoundland (overall mean) for 1984-1996 (O'Connell et al. 1996); North American mean for 1971-1995 (Anon. 1996).

[e]Return rate divided by ratio of river 1SW return proportion to North American 1SW return proportion

Table 3
Numbers of Alantic salmon returning after 1 sea winter, estimated number of smolts leaving North American rivers, and numbers of 1SW salmon in the sea prior to fishing mortality.

Smolt year (Yr)	North American 1SW returns in Yr+1[a]	Return rate (percent), wild smolts to 1SW[b]	North American smolt run in Y	North American pre-fishery maturing 1SW in Yr+1[a]	North American pre-fishery non-maturing 1SW in Yr+1[a]	North American pre-fishery total 1SW in Yr+1
1977	253,529	2.3	11,123,726	408,520	330,077	738,597
1978	348,313	8.8	3,947,960	587,390	730,725	1,318,115
1979	455,533	4.1	11,064,102	838,092	639,192	1,477,284
1980	560,048	2.2	25,391,499	908,837	605,935	1,514,772
1981	467,402	2.4	19,264,643	761,207	503,481	1,264,688
1982	294,371	6.7	4,399,851	513,115	286,898	800,013
1983	336,119	1.6	20,780,439	512,873	296,450	809,323
1984	386,842	2.2	17,202,365	634,337	468,776	1,103,113
1985	506,947	3.7	13,605,732	812,048	505,066	1,317,114
1986	495,765	3.7	13,232,556	848,239	462,953	1,311,192
1987	559,399	4.8	11,713,300	823,410	370,526	1,193,936
1988	341,626	4.1	8,352,764	567,807	293,057	860,864
1989	399,743	4.1	9,708,190	549,267	256,969	806,236
1990	273,818	3.5	7,819,152	401,895	299,086	700,981
1991	475,802	3.2	14,783,255	506,855	179,755	686,610
1992	426,144	2.8	15,045,579	447,931	137,134	585,065
1993	312,227	4.0	7,782,740	325,400	161,214	486,614
1994	326,148	4.6	7,051,523	338,165	156,490	494,655
1995	458,860	4.5	10,256,088	471,416	126,588	598,004
1996	306,480	2.9	10,605,458	319,065	97,899	416,964
1997[c]	349,451	3.0	11,575,497	412,480		
Mean 1977-1996	399,256	4	12,156,546	578,793	345,414	924,207
Mean 1990-1996	368,497	4	10,477,685	401,532	165,452	566,985

[a]From Anon. 1999a

[b]From Table 2

[c]Returns for Labrador are estimated from returns from other regions, using the ratio of Labrador returns:returns for other regions averaged for 1978-1996 (0.20)

Table 4
Fork length, weight, and number of North American Atlantic salmon alive from river exit to sea age 1 year, by month.

Smolt year (Yr)	Daily mortality per g (M_d)	Date Jun 1	Jun 15	Jul 15	Aug 15	Sep 15	Oct 15	Nov 15	Dec 15	Jan 15	Feb 15	Mar 15	Apr 15	May 15
Individual measures														
Fork length (cm)		13.8	14.8	18.6	25.1	32.9	38.7	42.0	43.5	44.1	44.4	44.7	45.6	47.4
Weight (g)		21	36	93	211	412	653	872	1007	1079	1112	1130	1165	1245
Numbers														
0% mortality at river exit														
1977	0.0441	11,123,726	8,867,341	6,025,172	4,445,067	3,490,841	2,868,247	2,393,728	2,031,886	1,724,116	1,466,577	1,268,384	1,081,166	928,331
1978	0.0179	3,947,960	3,601,975	3,060,669	2,723,991	2,470,287	2,281,563	2,120,593	1,984,472	1,856,964	1,739,315	1,640,094	1,537,478	1,445,543
1979	0.0328	11,064,102	9,350,094	7,018,004	5,599,398	4,679,739	4,044,640	3,536,436	3,131,045	2,771,784	2,458,062	2,206,875	1,960,118	1,750,407
1980	0.0459	25,391,499	20,060,608	13,424,367	9,785,595	7,611,940	6,206,022	5,142,454	4,336,510	3,656,247	3,090,293	2,657,394	2,250,915	1,921,127
1981	0.0443	19,264,643	15,342,305	10,407,869	7,666,597	6,016,265	4,939,183	4,118,922	3,493,544	2,962,626	2,518,373	2,176,712	1,854,179	1,591,050
1982	0.0277	4,399,851	3,815,461	2,992,617	2,471,822	2,123,468	1,876,795	1,675,115	1,511,041	1,362,895	1,231,105	1,123,722	1,016,388	923,532
1983	0.0528	20,780,439	15,842,798	9,976,950	6,933,061	5,191,993	4,104,306	3,305,592	2,716,582	2,232,083	1,839,196	1,545,867	1,276,943	1,064,051
1984	0.0446	17,202,365	13,677,136	9,251,979	6,801,728	5,326,722	4,366,787	3,636,754	3,080,874	2,609,524	2,215,587	1,912,965	1,627,603	1,395,087
1985	0.0381	13,605,732	11,186,651	8,012,659	6,161,837	5,001,299	4,220,955	3,610,659	3,133,910	2,719,721	2,365,104	2,086,413	1,817,634	1,593,488
1986	0.0376	13,232,556	10,907,329	7,846,285	6,054,365	4,927,312	4,167,620	3,572,223	3,106,216	2,700,621	2,352,729	2,078,856	1,814,274	1,593,244
1987	0.0372	11,713,300	9,677,990	6,990,183	5,410,989	4,414,863	3,741,872	3,213,379	2,796,988	2,437,696	2,127,276	1,882,507	1,645,665	1,447,486
1988	0.0370	8,352,764	6,908,834	4,999,274	3,875,464	3,165,657	2,685,601	2,308,260	2,012,179	1,753,817	1,531,663	1,356,363	1,186,618	1,044,477
1989	0.0405	9,706,190	7,885,135	5,531,454	4,184,586	3,352,493	2,799,607	2,371,587	2,040,326	1,755,073	1,512,981	1,324,295	1,143,805	994,550
1990	0.0392	7,819,152	6,391,743	4,533,180	3,459,056	2,790,267	2,343,103	1,996,070	1,724,393	1,490,221	1,290,563	1,134,270	984,120	859,404
1991	0.0500	14,783,255	11,437,009	7,384,621	5,233,535	3,980,972	3,187,207	2,597,153	2,157,125	1,791,314	1,491,531	1,265,471	1,056,175	888,804
1992	0.0528	15,045,579	11,469,398	7,221,527	5,017,591	3,757,126	2,969,765	2,391,637	1,965,332	1,614,696	1,330,382	1,118,128	923,545	769,518
1993	0.0451	7,782,740	6,173,254	4,159,162	3,047,999	2,381,018	1,947,943	1,619,236	1,369,394	1,157,906	981,452	846,118	718,704	615,045
1994	0.0432	7,051,523	5,647,149	3,867,407	2,870,888	2,265,705	1,869,070	1,565,604	1,333,253	1,135,202	968,815	840,366	718,659	618,984
1995	0.0463	10,256,088	8,066,595	5,392,988	3,920,607	3,043,212	2,476,822	2,049,069	1,725,424	1,452,646	1,226,032	1,052,930	890,613	759,101
1996	0.0527	10,605,458	8,092,113	5,103,093	3,550,074	2,660,879	2,104,935	1,696,413	1,394,961	1,146,851	945,537	795,151	657,203	547,935
Mean[a]	0.0419	12,156,546	9,801,205	6,789,727	5,085,928	4,042,713	3,354,501	2,824,983	2,417,469	2,068,416	1,773,746	1,545,227	1,327,713	1,148,752
Mean[b]	0.0475	10,477,685	8,210,954	5,419,144	3,907,435	3,013,282	2,439,502	2,008,373	1,683,693	1,411,250	1,185,907	1,014,490	854,410	725,257
20% mortality at river exit														
1977	0.0405	11,123,726	7,227,402	5,069,475	3,834,753	3,072,005	2,565,228	2,172,926	1,869,326	1,607,900	1,386,044	1,213,136	1,047,747	910,985
1978	0.0142	3,947,960	2,935,827	2,592,038	2,350,006	2,173,925	2,040,555	1,925,017	1,825,917	1,731,828	1,643,840	1,568,691	1,489,991	1,418,570
1979	0.0291	11,064,102	7,620,892	5,904,865	4,830,639	4,118,308	3,617,392	3,210,281	2,880,882	2,584,999	2,323,134	2,110,797	1,899,577	1,717,746
1980	0.0422	25,391,499	16,350,607	11,295,103	8,442,100	6,698,730	5,560,460	4,668,180	3,990,033	3,409,860	2,920,660	2,541,702	2,181,392	1,885,281
1981	0.0407	19,264,643	12,504,906	8,757,057	6,615,751	5,294,490	4,417,442	3,739,045	3,214,418	2,762,981	2,380,133	2,081,947	1,796,909	1,561,363
1982	0.0241	4,399,851	3,109,831	2,517,952	2,132,458	1,868,714	1,678,543	1,520,624	1,390,312	1,271,053	1,163,527	1,074,799	984,995	906,300
1983	0.0492	20,780,439	12,912,839	8,394,488	5,981,199	4,569,106	3,670,755	3,000,727	2,499,534	2,081,668	1,738,241	1,478,566	1,237,502	1,044,197
1984	0.0410	17,202,365	11,147,693	7,784,505	5,867,897	4,687,671	3,905,509	3,301,347	2,834,720	2,433,674	2,093,968	1,829,682	1,577,332	1,369,036
1985	0.0345	13,605,732	9,117,797	6,741,757	5,315,859	4,401,289	3,775,083	3,277,656	2,883,518	2,536,445	2,235,278	1,995,579	1,761,494	1,563,755
1986	0.0340	13,232,556	8,890,133	6,601,771	5,223,143	4,336,179	3,727,382	3,242,767	2,858,037	2,518,632	2,223,583	1,988,350	1,758,237	1,563,515
1987	0.0335	11,713,300	7,888,147	5,881,457	4,668,097	3,885,209	3,346,606	2,917,019	2,575,358	2,273,425	2,010,505	1,800,550	1,594,837	1,420,477
1988	0.0333	8,352,764	5,631,117	4,206,330	3,343,389	2,785,871	2,401,913	2,096,394	1,851,410	1,635,631	1,447,586	1,297,312	1,149,968	1,024,988
1989	0.0369	9,706,190	6,426,862	4,654,100	3,610,071	2,950,292	2,503,876	2,152,862	1,877,311	1,636,802	1,429,931	1,266,641	1,108,477	975,992
1990	0.0356	7,819,152	5,209,657	3,814,164	2,984,152	2,455,516	2,095,594	1,811,070	1,586,618	1,389,798	1,219,721	1,084,888	953,724	843,368
1991	0.0463	14,783,255	9,321,854	6,213,333	4,515,006	3,503,372	2,860,532	2,357,625	1,984,776	1,670,602	1,409,658	1,210,378	1,023,553	872,220
1992	0.0492	15,045,579	9,348,253	6,076,107	4,328,710	3,308,381	2,656,059	2,171,063	1,808,307	1,505,885	1,257,354	1,069,447	895,020	755,159
1993	0.0415	7,782,740	5,031,576	3,499,470	2,629,530	2,096,366	1,742,176	1,469,899	1,259,983	1,079,878	927,578	809,281	696,506	603,569
1994	0.0396	7,051,523	4,602,768	3,253,990	2,476,735	1,993,887	1,671,634	1,421,213	1,226,730	1,058,703	915,635	803,782	696,462	607,435
1995	0.0426	10,256,088	6,591,064	4,537,596	3,382,335	2,678,116	2,215,187	1,880,089	1,587,567	1,354,755	1,158,732	1,007,090	863,105	744,937
1996	0.0490	10,605,458	6,595,561	4,293,682	3,062,673	2,341,652	1,882,584	1,539,958	1,283,507	1,069,567	893,635	760,534	636,904	537,712
Mean[a]	0.0383	12,156,546	7,988,575	5,712,796	4,387,665	3,557,706	3,000,154	2,564,443	2,224,319	1,929,030	1,676,382	1,477,954	1,286,705	1,127,317
Mean[b]	0.0438	10,477,685	6,692,424	4,559,604	3,370,971	2,651,777	2,181,810	1,823,147	1,549,170	1,316,149	1,120,810	970,324	828,020	711,724

Table 4 (continued)

Smolt year (Yr)	Daily mortality per g (M_d)	Date: Jun 1	Jun 15	Jul 15	Aug 15	Sep 15	Oct 15	Nov 15	Dec 15	Jan 15	Feb 15	Mar 15	Apr 15	May 15
40% mortality at river exit														
1977	0.0358	11,123,726	5,552,467	4,057,575	3,169,938	2,605,351	2,221,360	1,918,086	1,679,043	1,469,593	1,288,745	1,145,479	1,006,214	889,130
1978	0.0095	3,947,960	2,255,455	2,074,650	1,942,595	1,843,694	1,767,019	1,699,252	1,640,053	1,582,860	1,528,444	1,481,204	1,430,927	1,384,538
1979	0.0245	11,084,102	5,854,767	4,726,215	3,993,172	3,492,715	3,132,461	2,833,760	2,587,630	2,362,644	2,160,052	1,993,077	1,824,277	1,676,537
1980	0.0376	25,391,499	12,561,389	9,040,526	6,978,528	5,661,158	4,806,422	4,120,698	3,583,878	3,116,552	2,715,632	2,399,950	2,094,921	1,840,052
1981	0.0360	19,264,643	9,606,921	7,009,091	5,468,808	4,490,229	3,825,284	3,300,531	2,887,215	2,525,316	2,213,050	1,965,836	1,725,679	1,523,905
1982	0.0194	4,399,851	2,389,134	2,015,352	1,762,763	1,584,847	1,453,534	1,342,286	1,248,789	1,161,720	1,081,849	1,014,857	945,950	884,557
1983	0.0445	20,780,439	9,920,316	6,718,893	4,944,264	3,875,034	3,178,691	2,648,603	2,245,100	1,902,808	1,616,218	1,396,106	1,188,447	1,019,146
1984	0.0363	17,202,365	8,564,239	6,230,667	4,850,604	3,975,589	3,381,976	2,914,166	2,546,167	2,224,335	1,946,974	1,727,640	1,514,806	1,336,192
1985	0.0298	13,605,732	7,004,767	5,396,056	4,394,270	3,732,710	3,269,033	2,893,256	2,589,997	2,318,266	2,078,364	1,884,285	1,691,667	1,526,240
1986	0.0293	13,232,556	6,829,864	5,284,014	4,317,628	3,677,490	3,227,726	2,862,457	2,567,111	2,301,965	2,067,489	1,877,459	1,688,540	1,526,006
1987	0.0288	11,713,300	6,060,086	4,707,480	3,858,809	3,295,025	2,897,994	2,574,912	2,313,204	2,077,871	1,869,370	1,700,133	1,531,617	1,386,399
1988	0.0286	8,352,764	4,326,116	3,366,719	2,763,760	2,362,682	2,079,937	1,849,647	1,662,951	1,494,936	1,345,967	1,224,961	1,104,362	1,000,398
1989	0.0322	9,708,190	4,937,451	3,725,111	2,984,208	2,502,127	2,166,232	1,900,376	1,686,215	1,496,006	1,329,551	1,195,999	1,064,537	952,578
1990	0.0309	7,819,152	4,002,330	3,052,832	2,466,802	2,082,510	1,814,680	1,596,668	1,425,112	1,270,251	1,134,098	1,024,383	915,916	823,136
1991	0.0417	14,783,255	7,161,535	4,973,111	3,732,259	2,971,191	2,468,419	2,081,123	1,782,741	1,526,901	1,310,701	1,142,875	982,979	851,295
1992	0.0445	15,045,579	7,181,815	4,883,276	3,578,260	2,804,125	2,300,015	1,916,442	1,624,235	1,376,352	1,169,089	1,009,804	859,541	737,043
1993	0.0368	7,782,740	3,865,519	2,800,953	2,173,659	1,777,069	1,508,637	1,297,510	1,131,726	986,989	862,463	764,147	668,896	589,089
1994	0.0349	7,051,523	3,536,087	2,604,472	2,047,354	1,691,005	1,447,552	1,254,533	1,101,858	987,636	851,358	758,955	668,854	592,862
1995	0.0380	10,256,088	5,063,599	3,631,862	2,795,954	2,271,296	1,918,242	1,641,936	1,425,964	1,238,222	1,077,390	950,924	828,891	727,066
1996	0.0443	10,605,458	5,067,054	3,436,635	2,531,710	1,985,942	1,630,224	1,359,352	1,152,856	977,566	830,902	718,118	611,657	524,812
Mean[a]	0.0336	12,156,546	6,137,240	4,572,484	3,626,994	3,017,272	2,597,984	2,263,686	1,997,900	1,763,099	1,558,701	1,395,528	1,235,699	1,100,272
Mean[b]	0.0391	10,477,685	5,141,469	3,649,477	2,786,560	2,248,958	1,869,339	1,609,329	1,391,476	1,202,937	1,042,130	916,208	795,197	694,650

[a]Mean 1977-1996

[b]Mean 1990-1996

Table 5
Biomass (t) of North American Atlantic salmon from river exit to sea age 1 year, by month.

Smolt year (Yr)	Date Jun 1	Jun 15	Jul 15	Aug 15	Sep 15	Oct 15	Nov 15	Dec 15	Jan 15	Feb 15	Mar 15	Apr 15	May 15	Jun 15	Jul 1	Mean
0% mortality at river exit																
1977	231	315	558	939	1,436	1,874	2,087	2,045	1,860	1,630	1,433	1,280	1,155	1,135	1,167	1,364
1978	82	128	285	575	1,017	1,490	1,849	1,998	2,003	1,933	1,853	1,792	1,799	1,935	2,082	1,435
1979	230	333	649	1,183	1,926	2,642	3,083	3,152	2,990	2,732	2,493	2,284	2,178	2,225	2,334	2,144
1980	528	714	1,242	2,067	3,132	4,054	4,483	4,366	3,944	3,435	3,002	2,623	2,391	2,334	2,393	2,907
1981	401	546	963	1,620	2,476	3,226	3,591	3,517	3,196	2,799	2,459	2,161	1,980	1,943	1,998	2,344
1982	92	136	277	522	874	1,226	1,460	1,521	1,470	1,368	1,270	1,184	1,149	1,195	1,264	1,050
1983	432	564	923	1,465	2,137	2,681	2,882	2,735	2,408	2,044	1,747	1,488	1,324	1,262	1,278	1,820
1984	358	487	856	1,437	2,192	2,653	3,170	3,102	2,815	2,463	2,161	1,897	1,736	1,702	1,749	2,067
1985	283	398	741	1,302	2,058	2,757	3,148	3,155	2,934	2,629	2,357	2,118	1,983	1,969	2,066	2,121
1986	275	388	726	1,279	2,028	2,722	3,114	3,127	2,913	2,615	2,349	2,114	1,983	1,992	2,071	2,104
1987	244	344	647	1,143	1,817	2,444	2,801	2,818	2,630	2,365	2,127	1,918	1,801	1,813	1,886	1,897
1988	174	246	463	819	1,303	1,754	2,012	2,026	1,892	1,702	1,532	1,383	1,300	1,309	1,363	1,365
1989	202	280	512	884	1,380	1,829	2,067	2,054	1,893	1,682	1,496	1,333	1,238	1,231	1,274	1,375
1990	163	227	419	731	1,148	1,531	1,739	1,736	1,606	1,434	1,282	1,147	1,070	1,068	1,108	1,165
1991	308	407	683	1,106	1,638	2,082	2,264	2,172	1,932	1,658	1,430	1,231	1,106	1,065	1,084	1,444
1992	313	408	668	1,060	1,546	1,940	2,085	1,979	1,742	1,479	1,263	1,076	958	913	924	1,317
1993	162	220	385	644	980	1,272	1,412	1,379	1,249	1,091	956	837	765	749	769	918
1994	147	201	358	606	932	1,221	1,365	1,342	1,225	1,077	949	837	770	759	782	896
1995	213	288	499	828	1,252	1,618	1,786	1,737	1,567	1,383	1,190	1,038	945	921	944	1,156
1996	221	288	472	750	1,095	1,375	1,479	1,404	1,237	1,051	898	766	682	650	659	934
Mean 1977-1996	253	349	628	1,074	1,684	2,191	2,483	2,434	2,231	1,972	1,746	1,547	1,430	1,415	1,480	1,626
Mean 1990-1996	218	292	501	825	1,240	1,594	1,751	1,695	1,522	1,318	1,146	996	903	876	896	1,128
20% mortality at river exit																
1977	231	257	469	810	1,264	1,676	1,894	1,882	1,735	1,541	1,371	1,221	1,134	1,128	1,167	1,260
1978	82	104	240	496	895	1,333	1,678	1,838	1,868	1,827	1,772	1,736	1,765	1,923	2,082	1,344
1979	230	271	546	1,020	1,695	2,363	2,799	2,900	2,789	2,582	2,385	2,213	2,138	2,212	2,334	1,993
1980	528	582	1,045	1,783	2,757	3,626	4,069	4,017	3,679	3,246	2,872	2,542	2,346	2,319	2,393	2,683
1981	401	445	810	1,398	2,179	2,886	3,259	3,236	2,981	2,646	2,352	2,094	1,943	1,931	1,998	2,166
1982	92	111	233	450	769	1,096	1,326	1,400	1,371	1,293	1,214	1,148	1,128	1,187	1,264	979
1983	432	459	777	1,264	1,880	2,398	2,616	2,516	2,246	1,932	1,671	1,442	1,300	1,254	1,278	1,673
1984	358	397	720	1,240	1,929	2,551	2,878	2,854	2,625	2,328	2,067	1,838	1,704	1,692	1,749	1,909
1985	283	324	624	1,123	1,811	2,466	2,857	2,903	2,736	2,485	2,255	2,053	1,946	1,976	2,066	1,966
1986	275	316	611	1,103	1,784	2,435	2,827	2,877	2,717	2,472	2,247	2,049	1,946	1,979	2,071	1,951
1987	244	281	544	986	1,599	2,186	2,543	2,593	2,453	2,235	2,034	1,858	1,768	1,801	1,886	1,760
1988	174	200	389	706	1,146	1,569	1,827	1,864	1,765	1,609	1,466	1,340	1,278	1,301	1,363	1,266
1989	202	229	431	763	1,214	1,636	1,877	1,890	1,766	1,589	1,431	1,292	1,215	1,223	1,274	1,273
1990	163	185	353	630	1,010	1,369	1,579	1,597	1,499	1,356	1,226	1,111	1,050	1,062	1,108	1,079
1991	308	332	575	954	1,442	1,862	2,055	1,998	1,802	1,567	1,368	1,193	1,086	1,058	1,084	1,330
1992	313	333	562	914	1,361	1,735	1,893	1,821	1,625	1,398	1,208	1,043	940	907	924	1,211
1993	162	179	324	555	862	1,138	1,281	1,268	1,165	1,031	914	812	751	745	769	848
1994	147	164	301	523	820	1,092	1,239	1,235	1,142	1,018	908	812	756	754	782	828
1995	213	234	420	715	1,102	1,447	1,621	1,598	1,462	1,288	1,138	1,006	927	915	944	1,067
1996	221	235	397	647	964	1,230	1,342	1,292	1,154	993	859	742	669	646	659	859
Mean 1977-1996	253	284	529	927	1,464	1,960	2,236	2,239	2,081	1,863	1,670	1,499	1,403	1,406	1,460	1,505
Mean 1990-1996	218	238	422	712	1,091	1,425	1,589	1,560	1,420	1,246	1,096	985	886	871	896	1,061
40% mortality at river exit																
1977	231	198	375	670	1,072	1,451	1,672	1,690	1,585	1,432	1,294	1,172	1,107	1,119	1,167	1,141
1978	82	80	192	410	759	1,154	1,481	1,651	1,708	1,699	1,674	1,667	1,723	1,908	2,082	1,239
1979	230	208	437	844	1,437	2,046	2,470	2,605	2,549	2,401	2,252	2,126	2,087	2,194	2,334	1,820
1980	528	447	837	1,474	2,338	3,140	3,592	3,608	3,362	3,019	2,712	2,441	2,290	2,301	2,393	2,426
1981	401	342	649	1,155	1,848	2,499	2,877	2,907	2,724	2,460	2,221	2,011	1,897	1,916	1,998	1,962
1982	92	85	186	372	652	950	1,170	1,257	1,253	1,203	1,147	1,102	1,101	1,178	1,264	897
1983	432	353	622	1,044	1,595	2,076	2,309	2,260	2,053	1,796	1,577	1,385	1,268	1,244	1,278	1,506
1984	358	305	577	1,025	1,636	2,209	2,540	2,563	2,400	2,164	1,952	1,765	1,663	1,678	1,749	1,729
1985	283	249	499	928	1,536	2,135	2,522	2,607	2,501	2,310	2,129	1,971	1,899	1,960	2,066	1,788
1986	275	243	489	912	1,513	2,108	2,495	2,584	2,483	2,298	2,121	1,968	1,899	1,964	2,071	1,775
1987	244	216	436	815	1,356	1,893	2,245	2,329	2,242	2,078	1,921	1,785	1,725	1,787	1,886	1,602
1988	174	154	312	584	972	1,359	1,612	1,674	1,613	1,496	1,384	1,287	1,245	1,290	1,363	1,152
1989	202	176	345	630	1,030	1,416	1,657	1,698	1,614	1,478	1,351	1,240	1,186	1,214	1,274	1,156
1990	163	142	282	521	857	1,185	1,394	1,435	1,370	1,261	1,157	1,067	1,024	1,053	1,108	981
1991	308	255	460	788	1,223	1,612	1,814	1,795	1,647	1,457	1,291	1,145	1,059	1,050	1,084	1,200
1992	313	255	450	756	1,154	1,502	1,671	1,635	1,485	1,299	1,141	1,002	917	900	924	1,090
1993	162	138	259	459	731	986	1,131	1,139	1,065	959	863	779	733	739	769	768
1994	147	126	241	433	696	946	1,094	1,109	1,044	946	857	779	738	748	782	751
1995	213	180	336	591	935	1,253	1,431	1,436	1,336	1,198	1,074	966	905	908	944	965

Table 6
Sizes of prey captured by seals in eastern Canada.

Predator	Prey	Prey length (cm) in predator samples			Prey length (cm) from trawl surveys			Location	Source
		Minimum	Maximum	N	Minimum	Maximum	N		
Grey seal	Fish	10-20	50-60					NW Gulf	Murie and Lavigne 1992
	Cod	10-15	79.7					Anticosti I	Benoit and Bowen 1990a
	Plaice	<10	>35					Anticosti I	Benoit and Bowen 1990a
	Lumpfish	<16	>28					Anticosti I	Benoit and Bowen 1990a
	Mackerel	<27	>45					Anticosti I	Benoit and Bowen 1990a
	Herring	<22	>36					Anticosti I	Benoit and Bowen 1990a
	Capelin	10-11	>17					Anticosti I	Benoit and Bowen 1990a
	Cod	10-15	55-60	115				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Pollock	5-10	35-40	55				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Silver hake	10-15	45-50	43				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Herring	5-10	40-45	160				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Sand lance	5-10	25-30	139				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Squid	10-15	25-30	78				Grand Manan, eastern NS, Sable I	Bowen et al. 1993
	Cod	0-5	45-50	81	5-10	45-50		Sable I	Bowen and Harrison 1994
	Redfish	10-15	25-30	71	5-10	30-35		Sable I	Bowen and Harrison 1994
	Silver hake	15-20	35-40	30	20-25	35-40		Sable I	Bowen and Harrison 1994
	Plaice	15-20	40-45	23	5-10	40-45		Sable I	Bowen and Harrison 1994
	Yellowtail	10-15	40-45	27	15-20	40-45		Sable I	Bowen and Harrison 1994
	Sand lance	3-7	28-32	876				Sable I	Bowen and Harrison 1994
Harbour seal	Cod	5-10	50-55					Bay of Fundy	Bowen and Harrison 1996
	Pollock	5-10	30-35					Bay of Fundy	Bowen and Harrison 1996
	Herring	10-15	35-40					Bay of Fundy	Bowen and Harrison 1996
	Squid	5-10	20-25					Bay of Fundy	Bowen and Harrison 1996
	Cod	10-15	35-40					E Cape Breton, Eastern Shore NS	Bowen and Harrison 1996
	Pollock	10-15	35-40					E Cape Breton, Eastern Shore NS	Bowen and Harrison 1996
	Herring	15-20	35-40					E Cape Breton, Eastern Shore NS	Bowen and Harrison 1996
	Squid	15-20	25-30					E Cape Breton, Eastern Shore NS	Bowen and Harrison 1996
Harp seal	Cod	24-26	54-56	90	30-32	75-77	17,088	Newfoundland	Lawson and Stenson 1997
	Cod		50.5	212				Newfoundland	Lawson and Stenson 1997
	Cod	10	57.1	390				Newfoundland	Lawson et al. 1995
	Herring	6	37	340				Newfoundland	Lawson et al. 1995
	Capelin	3	18	2,220				Newfoundland	Lawson et al. 1995
	Arctic cod	2	30	3,369				Newfoundland	Lawson et al. 1995
	Capelin	8.8	15.7	270				St. Lawrence estuary	Beck et al. 1993
Hooded seal	Redfish	24	48.1	29				Newfoundland	Ross 1992
	Greenland halibut	18.6	45.1	57				Newfoundland	Ross 1992
	Herring	21.8	35.6	22				Newfoundland	Ross 1992
	Capelin	14.8	16.9	5				Newfoundland	Ross 1992
	Arctic cod	13.4	24.9	23				Newfoundland	Ross 1992

Table 7
Sizes of prey captured by seabirds which potentially prey on salmon in eastern Canada.

Predator	Prey	Prey size in predator samples[a]			Prey length (cm) available			Location	Source
		Minimum	Maximum	N	Minimum	Maximum	N		
Northern Fulmar	Redfish	2.7	11.9	90				Barents Sea	Erikstad 1990
	Cod	1.9	13.6	31				Barents Sea	Erikstad 1990
	Polar cod	4.0	13.2	32				Barents Sea	Erikstad 1990
	Polar cod	9.3	11.0	7				Svalbard	Gjertz et al. 1985
	Sand lance	0	17	795	5	17	231	Shetland	Fowler and Dye 1987
	Discarded haddock	15	30	40	19	36	2,859	Shetland	Hudson and Furness 1988
	Discarded whiting	14	29	36	18	36	2,589	Shetland	Hudson and Furness 1988
Greater shearwater	*Illex* squid		20					Bay of Fundy	Brown et al. 1981
	Mackerel		20					Bay of Fundy	Brown et al. 1981
Black-legged kittiwake	Fish	6	16					Alaska	Baird 1994
	Cod	3.6	13.4	53	7	14	333	Barents Sea	Erikstad 1990
	Redfish	4.8	6.2	37	5	14	1,125	Barents Sea	Erikstad 1990
	Arctic cod	6.7	13.7	44	5	14	141	Barents Sea	Erikstad 1990
	Fish	6-8	14-16	9				Norway	Furness and Barrett 1985
Herring gull	Capelin	28 g	49 g	41				Witless Bay, Newfoundland	Pierotti 1983
	Squid	68 g	121 g	24				Witless Bay, Newfoundland	Pierotti 1983
	Smelt	7	17.4	86				Southern Ontario	Ewins et al. 1994
	Alewife	7.5 g	19.9	5				Southern Ontario	Ewins et al. 1994
	Red drum	16	23	615				Southern Ontario	Ewins et al. 1994
	Fish	10-12	14-16	5				Norway	Furness and Barrett 1985
	Discarded haddock	22	31	38	19	36	2,859	Shetland	Hudson and Furness 1988
	Discarded whiting	15	30	44	18	36	2,589	Shetland	Hudson and Furness 1988
Great black-backed gull	Discarded haddock	19	38	1126	19	36	2,859	Shetland	Hudson and Furness 1988
	Discarded whiting	20	39	1025	18	36	2,589	Shetland	Hudson and Furness 1988
Glaucous gull	Cod	4.4	5.3	3	7	14	333	Barents Sea	Erikstad 1990
	Redfish	5.4	5.7	4	5	14	1,125	Barents Sea	Erikstad 1990
	Arctic cod	7.6	13.5	13	5	14	141	Barents Sea	Erikstad 1990
Common murre	Capelin[b]	8.3	18.3	47				Gannet Islands, Labrador	Bradstreet 1983
	Sand lance[b]	6.2	13.2	36				Gannet Islands, Labrador	Bradstreet 1983
	Capelin	8-10	16-18	2,261				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Daubed shanny	10-12	16-18	394				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Arctic cod	6-8	14-16	179				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Fish	11	17	1,580				Norway	Furness and Barrett 1985
	Capelin	13.0	16.9	68	13.7 cm	16.5 cm	92	Norway	Erikstad and Vader 1989
	Smelt		22					Netherlands (lab study)	Swennen and Duiven 1977
	Fish		20					Theoretical calculations	Bradstreet and Brown 1985
	Fish		113 g					Laboratory observations	Golovkin 1963, quoted by Bradstreet and
Thick-billed murre	Capelin	8-10	16-18	168				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Arctic cod	8-10	14-16	8				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Daubed shanny	8-10	18-20	313				Gannet Islands, Labrador	Birkhead and Nettleship 1987
	Arctic cod	4-6	18-20	176				Hudson Strait, Hudson Bay	Gaston and Noble 1985
	Food	0.7 g	41.5 g	212				Hudson Strait, Hudson Bay	Gaston 1985
	Food	2.8	19.3	140				Prince Leopold I, Lancaster Sound	Gaston and Nettleship 1981
	Cod	3.2	12.1	42				Barents Sea	Erikstad 1990
	Arctic cod	11.1	14.3	8				Barents Sea	Erikstad 1990
	Fish	11	11	50				Norway	Furness and Barrett 1985
	Capelin	12.5	18.5	43	12.9 cm	16.5 cm	136	Norway	Erikstad and Vader 1989

[a]Prey sizes in cm except where noted
[b]Includes fish from razorbill and Atlantic puffin samples

Table 8
Vulnerability windows of Atlantic salmon to seal and seabird predation

Predator	Prey	Susceptible prey sizes		Geographic overlap		Vulnerability window
		Lengths (cm)	Dates	Area	Dates	
Grey seal	Post-smolt	All	All	Gulf, Scotian Shelf	1 Jun-31 Oct	1 Jun-31 Oct
	1SW	All	All	Gulf, Scotian Shelf	15 May-31 Oct	15 May-31 Oct
Harbour seal	Post-smolt	All	All	Lab, Nfld, Gulf, Scotian Shelf	1 Jun-31 Dec	1 Jun-31 Dec
	1SW	All	All	Lab, Nfld, Gulf, Scotian Shelf	1 Jan-31 Dec	1 Jan-31 Dec
Harp seal	Post-smolt	All	All	Lab, Nfld, Gulf	1 Jun-31 Dec	1 Jun-31 Dec
	1SW	All	All	Lab, Nfld, Gulf	1 Jan-31 Dec	1 Jan-31 Dec
Hooded seal	Post-smolt	All	All	Lab, Nfld, Gulf	1-31 Dec	1-31 Dec
	1SW	All	All	Lab, Nfld, Gulf	1 Jan-31 May, 1-31 Dec	1 Jan-31 May, 1-31 Dec
Northern fulmar	Post-smolt	≤ 17	1 Jun-4 Jul	Lab Sea, N&S Lab Banks, Nfld Banks[a]	1 Jan-31 Dec	1 Jun-4 Jul
Shearwaters	Post-smolt	≤ 20	1 Jun-22 Jul	Lab Sea, N&S Lab Banks, Nfld Banks, Scotian Shelf	May-Nov	1 Jun-22 Jul
Black-legged kittiwake	Post-smolt	≤ 15	1-17 Jun	Lab Sea, N&S Lab Banks, Nfld Banks, Gulf	1 Jan-31 Dec	1-17 Jun
Gulls	Post-smolt	≤ 31	1 Jun-7 Sep	Lab Sea, N&S Lab Banks, Nfld Banks, Gulf, Scotian Shelf	1 Jan-31 Dec	1 Jun-7 Sep
Common murre	Post-smolt	≤ 17	1 Jun-4 Jul	Lab Sea, N&S Lab Banks, Nfld Banks, Gulf	1 Jan-31 Dec	1 Jun-4 Jul

[a]For bird predators, areas defined by Diamond et al. 1993 as follows: Labrador Sea - from the edge of the continental shelf to 45°W and 60°N; Northern Labrador Banks - the continental shelf from 60°N to 53°N; Southern Labrador Banks - the continental shelf from 53°N to 50°N; Newfoundland Banks - the continental shelf east, southeast, and south of Newfoundland.

Table 9
Records of salmon predation derived from stomach samples of seals and seabirds (other than northern gannets) in eastern Canada. Lengths are estimated from otolith size.

Predator	Location	Date	Number of stomachs containing salmon	Type of remains	Number of salmon per stomach	Salmon length (cm)			Comments	Source
						Mean	Range	N		
Grey seal	Miramichi estuary	Summer, 1950-1954	3	Fish	1	Adults			Uncertain if salmon were wild-caught or stolen from nets	Fisher and Mackenzie 1955
Grey seal	Miramichi estuary	~1968-1970	1	Fish	1	NA			Uncertain if salmon were wild-caught or stolen from nets	Mansfield and Beck 1977
Grey seal	Magdalen Islands	~1968-1970	1	Fish	1	NA				Mansfield and Beck 1977
Grey seal	Anticosti I.	4 Jul-20 Aug 1986	1	Otolith	6	43.0	35.7-52.1	5	Calculated size is smaller than expected for this location and time	Benoit and Bowen 1990a
Harbour seal	Murre Ledge, near Grand Manan I., Bay of Fundy	3 Jul 1990	1	Tag	1				Tag had been applied to a hatchery smolt that was released in the Stewiacke R, NS, in May 1990	B. Beck, DFO Science (retired), pers. comm.
Harp seal	Les Escoumins, St. Lawrence estuary	14-16 Apr 1989	1	Otolith, flesh	1	29.1[a]	-	1	Calculated size is unexpected for this location and time.	Beck et al. 1993
Harp seal	Brighton, Notre Dame Bay, Nfld	3 May 1993	1	Otolith	1	34		1	Calculated size is unexpected for this location and time. Seal was a male aged 23.	O'Connell et al. 1998, G. Stenson pers. comm.
Common murre	Witless Bay, eastern Newfoundland	13 Jul 1984	1	Tag	1				Tag had been applied to a smolt on the St. Croix River, May 1984	D. Methven and J. Piatt in Montevecchi et al. 1988.

[a]Salmon remains weighing 445 g were found in 1 stomach of a sample of 9 stomachs, whose pooled contents weighed 23,348 g. Hence salmon remains accounted for 445/(23348/9) = 0.17 of the contents of one stomach.

Table 10
Sight records of seal-salmonid interactions in Newfoundland and Labrador.

Predator	Location	Date	Number of seals observed	Observation	Possibility that salmon was stolen from a net[a]	Source
Grey seal	St. Marys Bay, Newfoundland	Jun 1980	1	Seal observed with adult salmon in its mouth	Yes	DFO technical staff
Harp seal	Twillingate, Newfoundland	Winter 1996	1	Seal observed on offshore ice with salmon kelt	No	DFO Fisheries Officer
Grey seal	White Bear River estuary, Labrador	Jul 1998	1	Seal observed with adult salmon in its mouth	No	DFO Fisheries guardian
Harbour seal	Waterford River, Newfoundland	Feb 1999	1	Seal observed with a salmon or trout parr in its mouth	No	Reddin
Grey seal	Paradise River estuary, Labrador	Jun-Jul 1999	1	Seal observed with adult salmon in its mouth	Yes	DFO technical staff
Grey seal	Southwest Tributary, Paradise River, Labrador	Jul 1999	1	Seal chasing adult salmon into trap	No	DFO technical staff at counting fence

[a]Marked Yes if commercial fisheries may have been operating in the vicinity; otherwise marked No.

Table 11
Sample sizes of seal diet studies in eastern Canada.

Predator	Sample size		Number of samples containing salmon	Date	Region	Location	Source
	Total samples	Samples containing food					
Grey seal	82	41	0	Jul-Dec 1983	Northern Gulf	St. Lawrence estuary, western Anticosti I	Murie and Lavigne 1992
	744	295	1	14 Jun-20 Aug 1982-1987	Northern Gulf	Anticosti I	Benoit and Bowen 1990a
	782	316	1	1983-1987	Northern Gulf	Anticosti, other unnamed locations	Benoit and Bowen 1990b (includes new and all previously published data)
		114	NA	May-Aug 1988	Northern Gulf	Anticosti I	Proust and Hammill unpubl., cited by Hammill and Mohn 1994
		100	NA	Aug-Sep 1992	Northern Gulf	Anticosti I	Proust and Hammill unpubl., cited by Hammill and Mohn 1994
	67	NA	1	Mostly 1968-1970	Southern Gulf	Magdalen Islands	Mansfield and Beck 1977
	>22	NA	3	May-Nov, 1950-1954 (stomachs containing salmon were collected in summer)	Southern Gulf	Miramichi estuary	Fisher and Mackenzie 1955
	<36	NA	2	Mostly 1968-1970	Southern Gulf	Miramichi estuary	Mansfield and Beck 1977
	58	NA	4	1950-1970	Southern Gulf	Miramichi estuary	Mansfield and Beck 1977, including data from Fisher and Mackenzie 1955
	18	NA	0	Mostly 1968-1970	Southern Gulf	Amet I	Mansfield and Beck 1977
	143	NA	5	1950-1970	Southern Gulf		Mansfield and Beck 1977, including data from Fisher and Mackenzie 1955
	194	89	5[a]	1950-1987	Southern Gulf	Locations indicated by Mansfield and Beck 1977 (including data from Fisher and Mackenzie 1955), unnamed coastal locations	Benoit and Bowen 1990b (includes new and all previously published data)
	35	7	0	Jan 1990-1991	Southern Gulf	St. Georges Bay	Baker et al. 1995
	<22	NA	0	May-Nov, 1950-1954	Scotian Shelf	East coast of NS	Fisher and Mackenzie 1955
	137-154	NA	0	Mostly 1968-1970	Scotian Shelf	Fouchu and Gabarouse Bay	Mansfield and Beck 1977
	62	NA	0	Mostly 1968-1970	Scotian Shelf	Camp I	Mansfield and Beck 1977
	606	213	0	1950-1987	Scotian Shelf	Coastal NS	Benoit and Bowen 1990b (includes new and all previously published data)

Table 11 (continued)

Predator	Sample size		Number of samples containing salmon	Date	Region	Location	Source
	Total samples	Samples containing food					
Grey seal		94	0	Sep 1988-Nov 1990	Scotian Shelf	Eastern shore NS	Bowen et al. 1993
		198	0	1988-1993	Scotian Shelf	Eastern shore NS	Mohn and Bowen 1996 (includes data from Bowen et al. 1993)
	247	47	0	1983-1984	Scotian Shelf	Sable I	Benoit and Bowen 1990b
		37	0	Feb-Dec 1990	Scotian Shelf	Sable I	Bowen et al. 1993
	393	365	0	Jul 1991- Jan 1993	Scotian Shelf	Sable I	Bowen and Harrison 1994
	44	17	3	May-Nov, 1950-1954	Southern Gulf, Scotian Shelf		Fisher and Mackenzie 1955
	446	207	5	1950-1970	Southern Gulf, Scotian Shelf		Mansfield and Beck 1977, including data from Fisher and Mackenzie 1955
		12	0	Sep 1988-Jun 1990	Fundy	Grand Manan	Bowen et al. 1993
	528	143	0	Sep 1988-Nov 1990	Fundy, Scotian Shelf		Bowen et al. 1993
Total		1315					
Total with full ID		1094					
Harbour seal	11	11	0	Jan-Feb 1998	S Gulf	PEI	Cairns et al. unpubl.
	201	120	0	Jun-Oct, 1950-1953	S Gulf, Scotian Shelf, Fundy	Pownal Bay, PEI; east coast NS; south NB	Fisher and Mackenzie 1955
	602	279	0		Eastern Canada		Boulva and McLaren 1979
	321	164	0[b]	Jan-Oct, 1988-1992	Fundy	Grand Manan	Bowen and Harrison 1996
	148	85	0	Feb-Nov, 1988-1992	Scotian Shelf	E Cape Breton, Eastern Shore NS	Bowen and Harrison 1996
Total	1283	659					
Harp seal		16	NA	Apr-Sep 1990-1992	Labrador	Inshore	Lawson et al. 1995
		239	NA	Oct-Mar 1990-1992	Labrador	Inshore	Lawson et al. 1995
		352	0	1982-1993	Labrador	Inshore	Lawson and Stenson 1995 (includes data from Lawson et al. 1995)
		58	0	Jan-Feb 1991-1995	Newfoundland and Labrador	>30 km from shore, shot	Lawson and Stenson 1997
		120	0	Jan-Feb 1986-1995	Newfoundland and Labrador	>30 km from shore, from trawlers	Lawson and Stenson 1997
		51	0	Mar 1980-1995	Newfoundland and Labrador	>30 km from shore, shot	Lawson and Stenson 1997
		69	0	Apr-May 1980-1995	Newfoundland and Labrador	>30 km from shore, shot	Lawson and Stenson 1997
		90	0	May-Jul 1986-1995	Newfoundland and Labrador	>30 km from shore, gillnetted	Lawson and Stenson 1997
		99	NA	Apr-Sep 1990-1993	Newfoundland	South coast, inshore	Lawson et al. 1995
		243	NA	Apr-Sep 1990-1993	Newfoundland	Northeast coast, inshore	Lawson et al. 1995

Table 11 (continued)

Predator	Sample size: Total samples	Sample size: Samples containing food	Number of samples containing salmon	Date	Region	Location	Source
Harp seal		308	NA	Oct-Mar 1990-1993	Newfoundland	Northeast coast, inshore	Lawson et al. 1995
		1355	0	1982-1993	Newfoundland	Northeast coast, inshore	Lawson and Stenson 1995 (includes data from Lawson et al. 1995)
		16	NA	Oct-Mar 1990-1993	Newfoundland	South coast, inshore	Lawson et al. 1995
		181	0	1982-1993	Newfoundland	South coast, inshore	Lawson and Stenson 1995 (includes data from Lawson et al. 1995)
	25	25	0	3 Jan-13 Feb 1983	Northern Gulf	Les Escoumins	Murie and Lavigne 1991
	41	41	0	20 Dec 1988-27 Feb 1989	Northern Gulf	Les Escoumins	Beck et al 1993
	10	9	1	14-16 Apr 1989	Northern Gulf	Les Escoumins	Beck et al 1993
	16	14	0	3-21 Dec 1989	Northern Gulf	Harrington Harbour	Beck et al 1993
	260	2	0	1-12 Jan, 1950-1952	Northern Gulf	La Tabatière	Fisher and Mackenzie 1955
	105	14	0	15-30 Jun 1953	Northern Gulf	Blanc Sablon	Fisher and Mackenzie 1955
		109	0	Apr-Sep 1990-1993	Northern Gulf	Newfoundland west coast, inshore	Lawson et al. 1995
		96	0	Oct-Mar 1990-1993	Northern Gulf	Newfoundland west coast, inshore	Lawson et al. 1995
		64	NA	1982-1993	Northern Gulf	Newfoundland west coast	Lawson and Stenson 1995
		241	NA	Nov-Jun 1985-1993	Northern Gulf	Newfoundland west coast	Stenson et al. 1997 (includes data from Lawson and Stenson 1995)
		126	NA	Nov-Jun 1985-1993	Northern Gulf	Newfoundland southwest coast	Stenson et al. 1997 (includes data from Lawson and Stenson 1995)
	199	45	0	Mar 1976-1984	Southern Gulf	Unspecified	Stewart and Murie 1986
	81	81	0	21 Apr-16 May 1952	Southern Gulf	Magdalen Islands	Fisher and Mackenzie 1955
	164	62	0	3-20 Mar 1989	Southern Gulf	Magdalen Islands	Beck et al. 1993
	64	3	0	17 Feb-5 Apr 1949-1952	Southern Gulf	SE of Magdalens, Port Hood NS, E of PEI, off Cape North, near St. Paul I.	Fisher and Mackenzie 1955
	100	1	0	4 Apr 1952	Scotian Shelf	East of Scatari Island	Fisher and Mackenzie 1955
Total[c]		3145					
Total with full ID		2083					
Hooded seal	201	89	0	Oct-Jun 1982-1990	Newfoundland	Mostly northeast coast	Stenson et al. 1991
	67	55	0	Jan-May 1991	Newfoundland	Mostly inshore on northeast coast	Ross 1992
	268	144	0				

[a]Benoit and Bowen 1990b indicate 2 salmon occurences, but Mansfield and Beck 1977 indicate 5 salmon occurences.

[b]A salmon tag was recovered from a seal stomach near Grand Manan (B. Beck, pers. comm.), but this was not reported in Bowen and Harrison 1996.

[c]As of April 1999, the number of published and unpublished harp seal stomach records in DFO files is ~8300, of which ~6100 contained food (G. Stenson, DFO, pers. comm.)

Table 12
Sample sizes of kittiwake, gull, murre, and shearwater diet studies in Atlantic Canada.

Predator	N	Number of samples containing salmon	Date	Region	Location	Source
Black-legged kittiwake	69[a]	NA	May-Sep 1966-1967	Newfoundland	Witless Bay	Threlfall 1968
	NA	0	Late Jun-Aug 1969-1970	Newfoundland	Gull I, Witless Bay	Maunder and Threlfall 1972
	24	0	Jul-Dec 1978-1984	Fundy	Quoddy area	Braune 1987
Great black-backed gull	32[a]	NA[b]	May-Sep 1966-1967	Newfoundland	Witless Bay	Threlfall 1968
	126[a]		1976-1978	Newfoundland	Witless Bay	Pierotti 1979 in Good 1998
	117	0	15 Jun-14 Jul 1994-1995	St. Lawrence R	Islands in mid-estuary	Rail et al. 1996
	82[c]	0	Jun-Aug 1969-1970	Scotian Shelf	Sable I	Lock 1973
Herring gull	401[a]	NA	May-Sep 1966-1967	Newfoundland	Witless Bay	Threlfall 1968
	305[c]	0	May-Aug 1976-1978	Newfoundland	Great I, Witless Bay	Pierotti 1983
	350	0	15 Jun-14 Jul 1994-1995	St. Lawrence R	Islands in mid-estuary	Rail et al. 1996
	22	0	Jul-Dec 1978-1984	Fundy	Quoddy area	Braune 1987
	96	0	7 Jun-22 Jul 1994	Southern Gulf	Carleton, Bay of Chaleur	Rail et al. 1996
	NA[d]	NA	15 May-26 Jul 1986	Southern Gulf	Kouchibouguac National Park	Martin and LaPierre 1986
	82[c]	0	Jun-Aug 1969-1970	Scotian Shelf	Sable I	Lock 1973
Herring/great black-backed gull	537[a]	NA	Mid May-mid Aug 1970-1971	Newfoundland	Gull I, Witless Bay	Haycock and Threlfall 1975
Common murre	33	0	22 Jun-10 Aug 1981	Labrador	Near Gannet Islands	Bradstreet 1983
	3,733	0	late Jul-Aug 1982-1983	Labrador	Gannet Islands	Birkhead and Nettleship 1987
	44	NA	Winter	Newfoundland		Tuck 1961
	889	0[e]	Jun-Aug 1982-1984	Newfoundland	Witless Bay	Piatt 1987
	1012[f]	NA[e]	late Jun-Jul 1982-1985	Newfoundland	Gull I, Witless Bay	Burger and Piatt 1990
Thick-billed murre	650	0	late Jul-Aug 1982-1983	Labrador	Gannet Islands	Birkhead and Nettleship 1987
	614	NA	Winter	Newfoundland		Tuck 1961
	46	0	Winter 1981, 1983	Newfoundland	Northeast coast	Gaston et al. 1983
	1,200	0	Winter 1984-1986	Newfoundland	Inshore waters	Elliot et al. 1990
Greater shearwater	38	0	26 June 1961	Newfoundland	Eastern Grand Banks	Brown et al. 1981
	15	0	2nd week Sep 1975	Newfoundland	Notre Dame Bay	Brown et al. 1981
	20	0	late June 1978	Newfoundland	Placentia Bay	Brown et al. 1981
	63	0	13 Aug-3 Sep 1974-1975	Fundy	Brier Island	Brown et al. 1981
Sooty shearwater	20	0	late June 1978	Newfoundland	Placentia Bay	Brown et al. 1981
	30	0	13 Aug-3 Sep 1974-1975	Fundy	Brier Island	Brown et al. 1981

[a]Fish in samples were not identified to species
[b]Great black-backed gulls were observed feeding on salmon which had been caught in surface-set gillnets.
[c]Some fish were not identified to species
[d]Most fish were not identified to species
[e]Data reported by Piatt 1987 and Burger and Piatt 1990 overlap. A salmon tag was found in a murre stomach (Montevecchi et al. 1988), but was not reported in either study.
[f]Fish other than capelin and sand lance were not identified

Table 13
Salmon consumption by seals and seabirds under various scenarios.

Predator	Total annual food consumption in Atlantic Canada (t)[a]	Prey consumption during vulnerability window (t)[b]	Mean salmon biomass during vulnerability window (t)[c]	Salmon consumption scenarios: Predator consumes 1% of salmon cohort		Predator consumes 10% of salmon cohort		Predator consumes entire salmon cohort	
				Percent salmon in predator diet	Fraction of prey that is salmon	Percent salmon in predator diet	Fraction of prey that is salmon	Percent salmon in predator diet	Fraction of prey that is salmon
Grey seal	280,403								
Post-smolt predation		117,539	798	0.0068	1/14,737	0.068	1/1,474	0.68	1/147
1SW predation		129,830	934	0.0072	1/13,904	0.072	1/1,390	0.72	1/139
Harbour seal	5,664								
Post-smolt predation		3,321	1,027	0.3093	1/323	3.093	1/32	30.93	1/3
1SW predation		5,664	934	0.1649	1/606	1.649	1/61	16.49	1/6
Harp seal	3,127,951								
Post-smolt predation		1,833,922	1,583	0.0009	1/115,821	0.009	1/11,582	0.09	1/1,158
1SW predation		3,127,951	934	0.0003	1/334,898	0.003	1/33,490	0.03	1/3,349
Hooded seal	399,633								
Post-smolt predation		33,941	1,583	0.0467	1/2,144	0.467	1/214	4.67	1/21
1SW predation		199,269	934	0.0047	1/21,335	0.047	1/2,134	0.47	1/213
Northern fulmar	586,051	26,635	255	0.0096	1/10,444	0.096	1/1,044	0.96	1/104
Shearwaters	481,693	105,897	310	0.0029	1/34,146	0.029	1/3,415	0.29	1/341
Black-legged kittiwake	195,538	5,609	212	0.0378	1/2,644	0.378	1/264	3.78	1/26
Gulls	282,330	68,901	509	0.0074	1/13,534	0.074	1/1,353	0.74	1/135
Common murre	671,526	98,287	255	0.0026	1/38,542	0.026	1/3,854	0.26	1/385
All predators	6,030,789								
Post-smolt predation		2,294,052	1,027	0.0004	1/223,363	0.004	1/22,336	0.04	1/2,234
1SW predation		3,462,714	934	0.0003	1/370,740	0.003	1/37,074	0.03	1/3,707

[a]For seals, estimates are for eastern Canadian waters up to the northern boundary of NAFO area 2J (data from Hammill and Stenson 1997). For seabirds, estimates are for eastern Canadian waters to 60°N (data from Diamond et al. 1993 as re-analysed in Table 12)
[b]For seals, estimates are from Hammill and Stenson 1997 pro-rated for the period of vulnerability. For seabirds, from Table 14.
[c]From the northwest Atlantic salmon biomass estimated from 1990-1996 data, and assuming 20% mortality upon river exit. For seal predation on 1SW salmon, biomass is the product of weight at 1 July in the 1SW year and mean pre-fishery abundance.

Table 14
Food consumption by seabirds in eastern Canada, based on an energetics model by Diamond et al. 1993.

Zone[a]	Area (km^2)	Jan-Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov-Dec	Total
Energy demand (kJ/m^2 per period)											
Labrador Sea[b]		0.25	1.58	0.23	0.12	0.23	0.48	0.10	0.19	0.57	3.74
N Labrador Banks		1.89	0.74	1.02	0.22	0.43	0.99	0.46	2.04	0.48	8.27
S Labrador Banks		1.29	0.44	1.10	u.75	0.97	1.55	0.44	1.24	2.43	10.21
Newfoundland Banks		0.26	1.33	1.44	1.07	0.72	1.67	0.34	0.98	0.39	8.20
Scotian Shelf		0.21	0.28	0.17	0.34	0.41	0.29	0.28	0.35	0.58	2.91
Gulf of St. Lawrence		0.16	0.33	0.51	0.59	0.33	0.43	0.50	0.11	0.00	2.96
Mean		0.68	0.78	0.75	0.51	0.52	0.90	0.35	0.82	0.74	6.05
Prey consumption (t) by zone[c]											
Labrador Sea	984,894	48,279	304,159	44,417	22,208	44,417	92,696	18,348	36,692	110,076	721,290
N Labrador Banks	129,693	48,063	18,818	25,939	5,595	10,935	25,178	11,698	51,877	12,206	210,306
S Labrador Banks	180,471	47,925	16,347	40,866	27,863	36,037	57,584	16,347	46,068	90,278	379,314
Newfoundland Banks	571,413	29,131	149,016	161,340	119,885	80,670	187,110	38,094	109,801	43,696	918,743
Scotian Shelf	133,106	5,481	7,308	4,437	8,874	10,701	7,569	7,308	9,135	15,137	75,948
Gulf of St. Lawrence	214,000	6,714	13,847	21,400	24,757	13,847	18,043	20,980	4,616	0	124,204
Total	2,222,578	185,592	509,494	298,399	209,182	196,606	388,178	112,773	258,188	271,394	2,429,606
Prey consumption (t) by main predator species[c]											
Northern fulmar											
Labrador Sea		39,589	22,508	20,210	14,014	15,901	28,180	11,540	26,235	67,917	246,092
N Labrador Banks		3,701	3,387	11,589	3,541	5,380	8,585	0	6,848	7,129	50,139
S Labrador Banks		33,548	12,996	11,770	1,337	12,793	20,558	2,795	12,991	61,660	170,447
Newfoundland Banks		7,632	14,902	22,265	2,877	3,630	21,331	2,819	19,545	17,826	112,828
Scotian Shelf		378	146	679	204	43	0	58	393	802	2,704
Gulf of St. Lawrence		181		364	693	1,066	198	1,280	78		3,841
Total		85,009	53,938	66,855	22,667	38,813	78,851	18,492	66,090	155,336	586,051
Shearwaters											
Labrador Sea		0	0	0	4,486	14,480	46,348	789	220	0	66,323
N Labrador Banks		0	0	0	0	2,110	7,779	0	52	0	9,942
S Labrador Banks		0	0	0	3,539	16,505	25,798	7,552	1,106	1,083	55,582
Newfoundland Banks		0	298	13,230	31,889	47,837	142,204	24,037	58,744	5,025	323,264
Scotian Shelf		0	0	1,287	5,661	4,066	817	197	4,439	1,529	17,997
Gulf of St. Lawrence		0		0	74	1,952	1,732	4,825	0		8,584
Total		0	298	14,517	45,650	86,951	224,678	37,401	64,561	7,637	481,693
Kittiwakes											
Labrador Sea		2,221	20,987	5,019	89	10,394	7,045	3,431	5,174	36,105	90,464
N Labrador Banks		1,154	1,186	3,943	45	1,028	3,424	1,345	3,580	867	16,570
S Labrador Banks		2,636	441	409	1,588	1,586	4,088	2,387	15,064	9,118	37,317
Newfoundland Banks		3,612	13,411	5,486	2,278	645	1,684	1,181	9,004	4,850	42,151
Scotian Shelf		263	7	9	35	0	136	132	375	288	1,245
Gulf of St. Lawrence		671		1,562	1,609	1,592	992	944	420		7,792
Total		10,557	36,033	16,427	5,644	15,245	17,370	9,419	33,615	51,228	195,538
Gulls											
Labrador Sea		5,214	4,258	10,749	1,910	178	556	92	1,468	5,284	29,708
N Labrador Banks		2,740	9,202	7,107	0	350	2,014	3,439	2,334	2,075	29,262
S Labrador Banks		11,358	2,926	6,048	1,170	649	1,152	1,880	13,314	15,167	53,663
Newfoundland Banks		6,088	19,670	3,388	8,152	7,583	2,620	4,152	16,800	8,870	77,323
Scotian Shelf		3,623	6,022	1,358	2,078	5,907	6,085	3,135	2,393	12,171	42,769
Gulf of St. Lawrence		2,806		7,554	6,932	6,397	9,202	12,882	3,831		49,605
Total		31,829	42,078	36,204	20,241	21,063	21,629	25,580	40,140	43,566	282,330
Murres											
Labrador Sea		193	256,406	7,551	1,910	178	556	1,266	587	3,082	271,728
N Labrador Banks		144	9,221	3,320	2,008	940	1,133	0	38,130	1,477	56,374
S Labrador Banks		192	0	17,491	14,851	2,054	1,324	1,291	1,382	2,528	41,113
Newfoundland Banks		6,176	93,284	95,191	67,975	11,536	936	38	1,867	3,976	280,977
Scotian Shelf		428	175	204	9	0	0	0	9	30	855
Gulf of St. Lawrence		779		8,432	9,457	1,454	162	0	194		20,478
Total		7,911	359,086	132,188	96,210	16,162	4,111	2,595	42,168	11,094	671,526

[a]Diamond et al. 1993 define zones as follows: Labrador Sea - from the edge of the continental shelf to 45°W and 60°N; Northern Labrador Banks - the continental shelf from 60°N to 53°N; Southern Labrador Banks - the continental shelf from 53°N to 50°N; Newfoundland Banks - the continental shelf east, southeast, and south of Newfoundland.

[b]Figures given by Diamond et al. (1993) for the Labrador Sea are reduced by 50%, to compensate for overestimation due to the concentration of survey effort near the edge of the continental shelf, where birds tend to congregate.

[c]Energy demands (kJ/m^2) supplied by Diamond et al. 1993 were converted to harvests by assuming 1 g wet weight contains 5.1 kJ (mean of energy densities compiled by Cairns 1998).

Table 15

Estimated harvest of Atlantic salmon by grey, harbour, and harp seals and by common murres, based on post-1980 records of salmon predation (Table 10). Calculations are based on frequency of occurrence (except where noted), which may not accurately reflect the contribution of salmon to the diet.

Predator	Number of stomachs containing salmon	Number of salmon per stomach	Number of fish per food-containing stomach		Number of samples with full ID	Salmon as a percent of diet[a]	Total prey harvest in eastern Canada	Estimated salmon harvest (t)	Mean salmon biomass (t) during window of vulnerability	Salmon harvest as a percent of biomass	Salmon harvest estimates from Hammill and Stenson 1997	
			Mean	Source							Harvest (t)	Percent of biomass
	A	B	C		D	E						
Grey seal	1	6	1.41	Benoit and Bowen 1990a	1,094	0.389	280,403	1,089.6	934	116.7	712	76.2
Harbour seal	1	1	6.75	Bowen and Harrison 1996	648	0.023	5,664	1.3	934	0.1	0	0.0
Harp seal												
Brighton	1	1	26.82	Lawson et al. 1995	6,100	0.0006						
Escoumins	1	1			6,100	0.0028[b]						
Total						0.0034	3,127,953	106.3	934	11.4	2,474	264.9
Common murre	1	1	0.99	Platt 1987	3,766	0.027	248,672[c]	66.6	255	26.1	-	-

[a]Calculated as E=(100*A*B/C)/F

[b]Salmon constituted 0.17 of the prey contents of one stomach (Table 8). Salmon as a percent of diet was calculated as 100*0.17/6,100

[c]Based on estimated harvest by murres from May to August, to exclude wintering thick-billed murres.

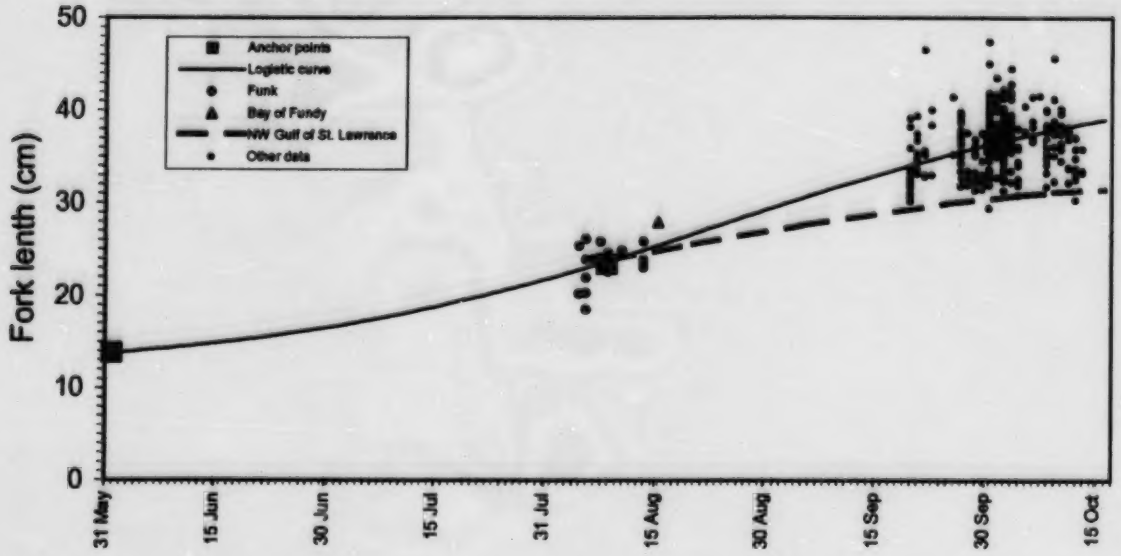

Fig. 1
Composite length growth of post-smolt Atlantic salmon, from river exodus to October. The logistic curve is fitted to anchor points representing mean lengths of smolts in the Miramichi River (Allen et al. 1972), of post-smolts captured by gannets on Funk Island in August (Montevecchi unpubl.), and of post-smolts captured in research cruises in the Labrador Sea in September-October. Bay of Fundy data are from Allen et al. 1972 and NW Gulf of St. Lawrence data are from Dutil and Coutu 1988.

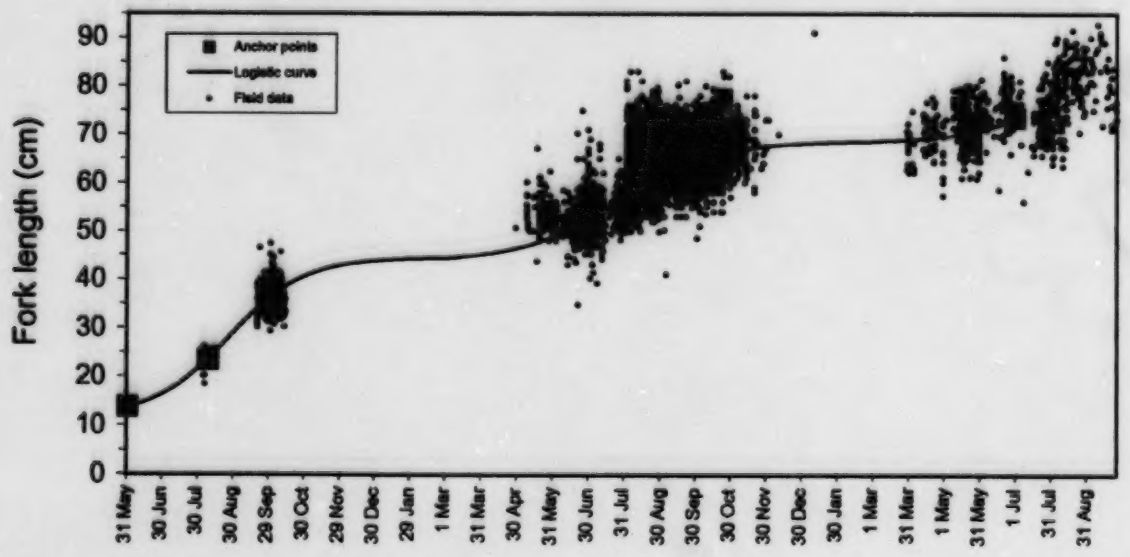

Fig. 2
Composite length growth of Atlantic salmon, sea age 0 to 2 years. The logistic curve is fitted to anchor points representing mean lengths of smolts in the Miramichi River (Allen et al. 1972), of post-smolts captured by gannets on Funk Island in August (Montevecchi unpubl.), of post-smolts taken in research cruises in the Labrador Sea in September-October, and of 1 sea winter and 2 sea winter virgin salmon returning to the Miramichi River (Moore et al. 1995).

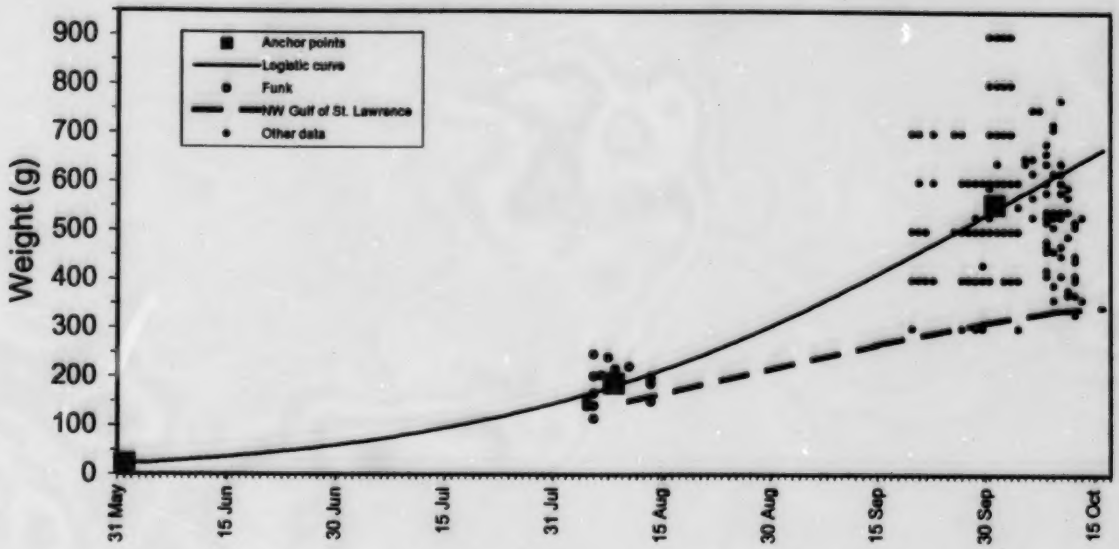

Fig. 3

Composite weight growth of post-smolt Atlantic salmon, from river exodus to October. The logistic curve is fitted to anchor points representing mean weights of smolts in the Miramichi River (R.A. Cunjak unpubl.), of post-smolts captured by gannets on Funk Island in August (Montevecchi unpubl.) and of post-smolts taken in research cruises in the Labrador Sea in September-October. NW Gulf of St. Lawrence data are from Dutil and Coutu 1988.

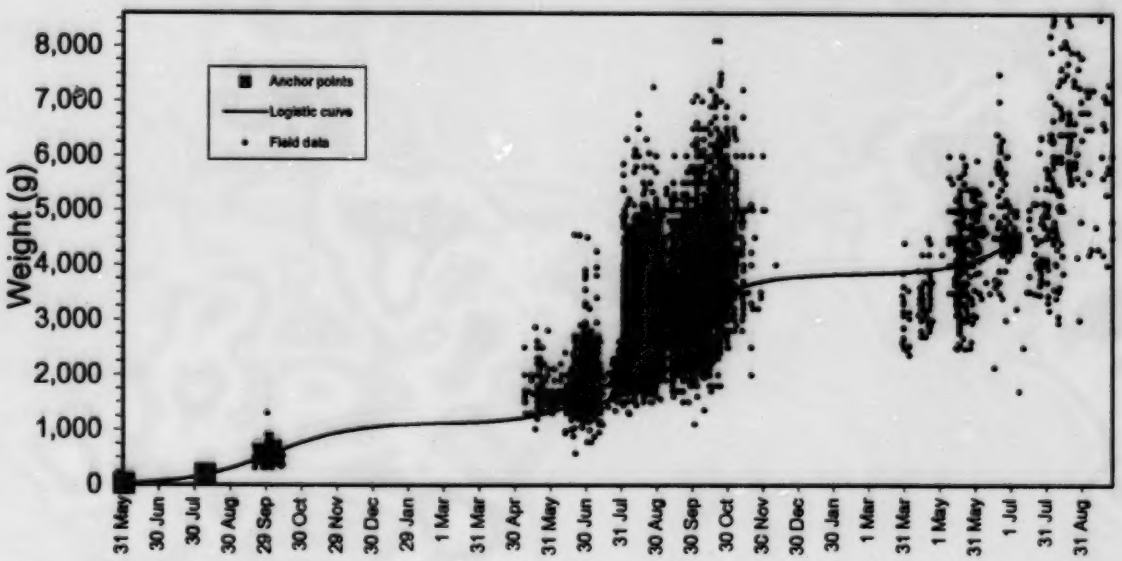

Fig. 4

Composite weight growth of Atlantic salmon, sea age 0 to 2 years. The logistic curve is fitted to anchor points representing mean weights of smolts in the Miramichi River (R.A. Cunjak unpubl.), of post-smolts captured by gannets on Funk Island in July-August (Montevecchi unpubl.), of post-smolts taken in research cruises in the Labrador Sea in September-October, and of 1 sea winter and 2 sea winter virgin salmon returning to the Miramichi River (Moore et al. 1995).

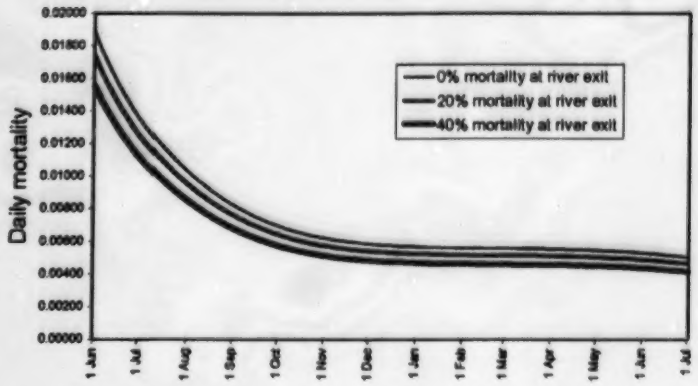

Fig. 5
Estimated daily instantaneous mortality of North American salmon from river exodus to sea age 1 year. Curves are calculated from the mean estimated smolt run and the mean estimated 1SW pre-fishery abundance for smolt years 1990 to 1996.

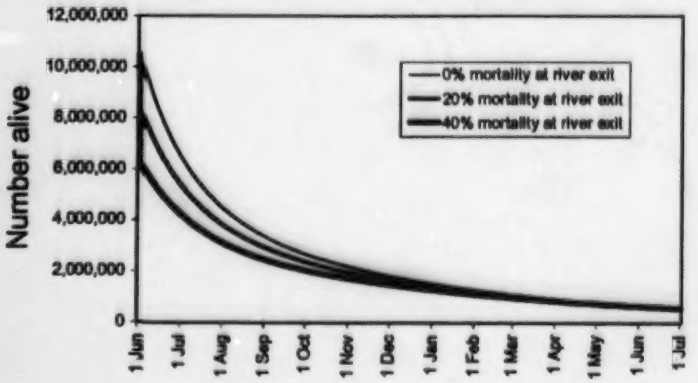

Fig. 6
Estimated number of North American salmon alive between river exit and sea age 1 year. Curves are calculated from the mean estimated smolt run and the mean estimated 1SW pre-fishery abundance for smolt years 1990 to 1996.

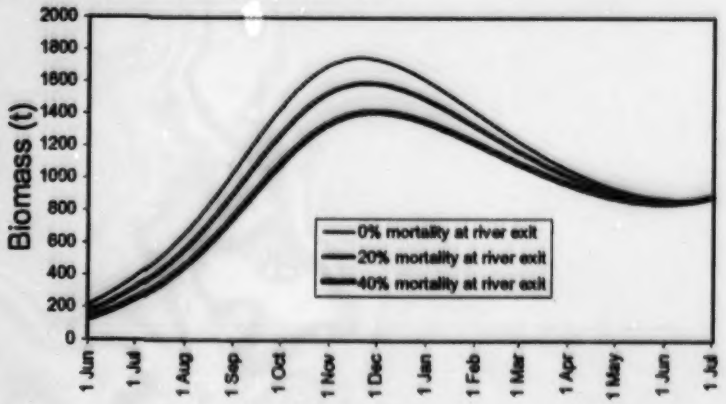

Fig. 7
Estimated biomass of North American Atlantic salmon from river exodus to sea age 1 year. Curves are calculated from the mean estimated smolt run and the mean estimated 1SW pre-fishery abundance for smolt years 1990 to 1996.